THE ROOK : ASPECTS OF ITS BEHAVIOUR AND ECOLOGY

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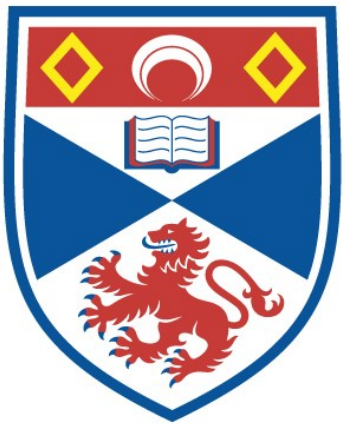

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by

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the degree of Ph.D. of the University of St. Andrews and that he is qualified to submit this thesis in application for that degree.

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I was admitted as a research student under Ordinance No. 12 on 1st October 1975 and as a candidate for the degree of Ph.D. on 1st October 1976; the higher study for which this is a record was carried out in the University of St. Andrews between 1976 and 1983.

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Contents

Preface

This thesis presents the results of studies on the rook and, to a lesser extent, the carrion crow. These were conducted in N.E. Fife from 1976 to 1979 and, as far as the size of the rook population is concerned, are still in progress.

Throughout the thesis Tables and Figures are numbered with respect to the chapter in which they appear. Thus, for instance, the first Table in chapter 4 is denoted Table 4.1, the second Figure in chapter 7 is Fig. 7.2, and so on. To help the reader find these every page in the thesis is numbered, including pages with Tables and Figures, and every time a Table or Figure is referred to its page number is given also. Tables and Figures appear at the end of the chapter to which they belong. There are ten chapters in the thesis.

The general biology of the rook and of the carrion crow are described in chapter 1 by way of introduction. The study area is also described here.

Chapter 2 is a region by region account of the decline in rook numbers in Great Britain since 1945, and some possible reasons for this decline are explored.

Chapter 3 addresses the results of rook population surveys in the study area of N.E. Fife. Some attention is paid to 1977 and 1979 sample surveys and (almost) complete surveys in 1975, 1980 and 1983, but the main focus of the chapter is centred on surveys conducted in 1945 and 1978. The geographical distribution of rookeries in these two years is investigated, and reasons for the difference discussed. The decline in rook numbers since 1945 is once again approached, this time with regard specifically to the N.E. Fife rook population. Possible causes of the decline are considered, with the emphasis on the changing pattern of agricultural land use.

In chapter 4 the results of research into habitat use of rooks and carrion crows are presented, and chapter 5 contains further quantification of this using niche breadth and overlap measures.

The diet of young rooks at one rookery in the study area is reported in chapter 6. The method used here was analysis of gizzard contents.

Following the finding of high degrees of overlap between rooks and carrion crows in chapters 4 and 5, chapter 7 is a study of competition between these two species in the condition of an aviary. A possible means by which subordinate individuals (as rooks are in relation to carrion crows) may compete successfully with dominant individuals is suggested.

Chapter 8 is a review of all known tool-using performances by birds, and the ecological circumstances under which tool-use is most likely to occur are postulated. This chapter serves as an introduction to chapter 9 which describes an example of tool-use by at least one captive rook. The proximate causation of this instance of tool-using behaviour is elucidated.

Finally, chapter 10 recaps on the results of the above mentioned studies and draws attention to the behavioural and ecological adaptability of the rook. Some topics for future research which could valuably contribute to a greater understanding of rook natural history are suggested.

Throughout the thesis scientific and vernacular names are given on first mention of a species. Thereafter only the vernacular is used unless it would be helpful to the reader to reiterate the scientific name.

Acknowledgments

I received many different sorts of assistance while conducting this research and completing the production of the thesis.

First of all, I thank my wife, Aileen, who gave me unwavering support at all stages of the project.

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Finally, I thank my supervisor for guidance, and for his help with all aspects of the research.

Abstract

Aspects of the ecology and behaviour of the rook Corvus frugilegus L. were studied.

The decline of rook populations in Britain since the 1940's is documented and the extent and reasons for the decline in north east Fife examined in detail. The most likely causes of this were changes in agricultural practices, including the way the land is used and possibly the use of organo-chlorine insecticides.

The ecological relationship between the rook and the carrion crow C. corone L. is explored in an investigation of their habitat use and associated niche metrics. Both species are heavily dependent on agricultural land, especially grassland, for foraging. The carrion crow narrows its niche breadth more than the rook does at times of possible food shortage. Observations on captive birds show rooks to be subordinate to carrion crows. Analysis of nestling rook gizzard contents revealed cereal to be an abundant food as well as invertebrates, particularly beetles and tipulids.

A review of tool-use in birds is presented and the conditions under which tool-use is likely to arise are elucidated. The proximate causation of an example of this category of behaviour performed by at least one captive rook is reported.

The rook is identified as an ecologically and behaviourally adaptable bird.

Chapter 1. Introduction

The study area of north-east Fife

The area with which this study is mainly concerned and which I now define as north east Fife is that part of the old county and new region of Fife north of approximately 56^{o} 10´ N and east of approximately 3^{o} 08´ W. The following parishes are included in this area: Anstruther and Carnbee (excluding the Isle of May), Balmerino, Cameron, Ceres, Crail, Creich, Cults and Cupar, Dairsie, Elie and St. Monance, Dunino, Ferry-Port on Craig, Flisk, Forgan, Kemback, Kennoway, Kettle, Kilconquhar, Kilmany, Kilrenny, Kingsbarns, Largo, Leuchars, Logie, Monimail and Moonzie, Newburgh and Scoonie, Newburn, Pittenweem (amalgamated with Elie and St. Monance in 1977) and St. Andrews and St. Leonards. These make up a total area of 52115.16 ha or 520.93 km^2. Land use in this mainly agricultural part of Scotland is predominantly arable with some mixed farms also. The best land is around the coast and the major crops are cereals. Easily the most abundant crop is barley, mainly the variety ´Golden Promise´. This is followed in order of abundance by grass, potatoes, wheat and then oats. The area devoted to all crops excluding grass is less than that devoted to barley. The land is only gently undulating, the highest point above sea level being only 300 m or so. There is consequently little land defined as rough grazings (mountain and heathland used for grazing). The only really extensive area of woodland is in the north at Tentsmuir, although there are many other smaller areas of woodland which would also appear to be unsuitable for the subjects of this study to nest in.

Geologically, two systems are represented in N.E. Fife. In the north of the area the underlying rocks belong to the Old Red Sandstone system while in the south and east they are mainly

Carboniferous. There are also some igneous intrusions in the central part of the area. The most fertile, loamy soils occur around the coastline and inland along the river Eden just north of the town of St. Andrews. To the south, soils are of a light loam, less fertile and contrasting with the more alkaline, fertile soils in the centre of the region. The area has a moderate climate. Mean temperature in winter is between 2 and 4 ^{o}C and in the summer between 12 and 14 ^{o}C. Average daily rainfall throughout the year varies between 1.50 and 3.00 mm (White & Smith 1982). Prevailing winds are mostly west or south-west but in springtime they tend to be easterly.

The rook

The rook, Corvus frugilegus L., is a member of the Corvidae, the crows. The genus Corvus contains the largest number of species in the family. Within it, Goodwin (1976) noted the difficulty of placing the rook phylogenetically, as did Jollie (1978) who thought it was related to a Eurasian (in origin) group of larger crows which included the carrion crow C. corone, the collared crow C. torquatus and the pied crow C. albus. Its true relationship to other congenerics remains unclear, however. The species is distributed between approximately 64^{o} N and 30^{o} S, and from Ireland in the west to China in the east, but in autumn and winter some populations migrate to northern Africa, the Middle East and northern India. It was introduced into New Zealand in the nineteenth century. In the British Isles the rook is almost ubiquitous, being sparse or absent in the breeding season only on high ground (> 2,500 ft), moorish, generally treeless areas, the centres of large cities and some islands.

It is a large bird, ranging from about 325 g to over 550 g in weight, with a total length of almost 500 mm and a wing span of

about twice that (Coombs 1978, Green 1981). Adult females are, on average, slightly smaller than males, but the sexes are alike with respect to plumage. This is black with a purple and green iridescence. The feathers of the tarsi are noticably "shaggy" in appearance. The bill and legs are also black and the eye is dark brown. The region around the base of the bill (nostrils, face and chin) is bare, revealing grey skin. Juveniles are similar to adults but duller in appearance without the gloss of the adults. They adopt the completely bare face region only after spring/early summer of their second calendar year. Adults of the eastern subspecies, C. f. dastinator, retain bristle feathers on the face and throat. The longest lived wild rook on record was over 19 years old at death (Hickling 1983), but lifespan is usually between 4 and 10 years (Burkitt 1936, Busse 1969).

The rook breeds colonially, usually in tall trees. The number of pairs nesting in colonies (rookeries) varies, and estimates of 20,000-30,000 have been made for rookeries in central Europe (see Malmberg 1971). The largest recorded rookery in Britain was in Aberdeenshire with 6,697 nests in 1957 (Watson 1967). Commonly, rookeries are much smaller than this and rarely, in Britain at least, reach more than 500 nests. Only four rookeries contained more than 1,000 nests in the United Kingdom in 1975, when the majority contained between 1 and 25 nests and the average rookery size was 31.97 nests (Sage & Vernon 1978).

In Britain the rook is fairly sedentary and non-migratory, and is found in flocks at all times of the year. Usually, they breed, feed and roost together. They are not territorial as such, only a small area around the nest being defended. The main focus of social activity in the breeding season is the rookery. The birds begin to roost in their own rookery in springtime. When young are in

the nest flocks feeding in fields are generally composed of males collecting food for themselves, their mates and their young. After the young have fledged, in summer, they accompany their parents to fields for foraging and are still fed by them to a large extent there. Adults also moult in the summer and a new summer roost is used, which may also be used by rooks from other rookeries. In autumn, another roost, generally a rookery site, is adopted by birds from several rookeries and a further change of roost is made in the winter, when rooks from many rookeries, as well as jackdaws, C. monedula, carrion/hooded crows and ravens C. corax, may gather in many thousands. This roost is used until about March when egg laying begins again (see Coombs 1961b and Patterson et al 1971 for accounts of rook roosting in Cornwall and Aberdeenshire respectively).

Rooks probably pair for life and are monogamous, although bigamy has been observed (Green 1982). Nest building may begin in February in the south of Britain, but it is usually in March in the north. This is done by both sexes, but the male appears to do most of it. The bird is single brooded and eggs are laid usually in March depending on latitude and temperature. Clutch size normally ranges from 3 to 5 eggs but extremes of 1 and 9 have been recorded. Average clutch size has been noted as being 4.3 in the south of England and 3.6 in south Scotland (Holyoak 1967). Lockie (1955) also recorded it as 4.3 in England (Oxfordshire) although late clutches (in April) averaged 3.5 eggs. Purchas (1979) found identical average clutch sizes to those of Lockie for rooks resident in part of New Zealand. There are too few data to reveal any relationship between clutch size and latitude (Holyoak 1967). Incubation, starting some time before completion of the clutch, lasts about 18 days, and is done by the female. Over 80% of eggs hatch. The fledging period lasts for about 32 days. The chances of young rooks surviving this

period decrease with increasing brood size. Lockie (1955), for example, found that only 59% of nestlings survived when there were four or more others in the nest, while 100% from nests containing only two nestlings did so. Males provide food for females and young at the nest. In summer, after fledging, families parties are discernible in fields containing feeding rook flocks. Mortality of juveniles is high in the summer and again in the winter (Holyoak 1971). Young rooks tend to disperse further than adults in the winter and visit their natal, and other, rookeries in late springtime, possibly prospecting for a site at which to breed the following year (Grace 1973). Occasionally, they may attempt to breed when one year old.

The rook's habitat may be categorised broadly as farmland. Its ecology is inextricably linked to agriculture, important feeding stations being grass fields and other fields devoted to growing crops. As with most corvids, rooks are omnivorous. They tend to feed on what is available and this includes large quantities of cereal of all kinds. Most of this is spillage and what is left in stubble fields after harvesting, but they will dig up newly sown grain. Many invertebrates are also eaten by rooks and a variety of species of earthworms, dipterous larvae and beetles (including larvae) are especially important. These items are taken either from the surface or are dug out from the sub-soil. Some vertebrate prey such as carrion, small mammals and birds and bird eggs also features in the diet. Scavenging is also a common feeding method in fields, roads, towns and the sea shore.

The main predator of the rook is man. Others include some of the larger birds of prey and, at least in continental Europe, some small carnivores.

The carrion crow

The rook is sympatric with either the carrion crow, Corvus corone corone, or the hooded crow, C. c. cornix, throughout its range. The hooded crow's range, however, extends further north and west in Europe to Iceland, and further south in Europe and also to Egypt, while the carrion crow's extends further south in Europe and further north and east in Asia and includes Japan. The hooded crow is thus the north and central European/western Asian form of Corvus corone and the carrion crow is the western European/eastern Asian form. In the British Isles the hooded crow occurs in Ireland and north and western Scotland while the carrion crow occurs elsewhere. There is a zone of overlap between the ranges of the two subspecies where they interbreed. As the present study deals with the carrion crow what follows refers to that subspecies but as the biology of carrion and hooded crows is similar most will pertain to the latter as well. Plumage coloration is the major exception.
Phylogenetically, the species has been placed in close relation to the collared crow, and has been also with the pied crow and the common crow C. brachyrhynchos. Like the rook it is ubiquitous in the British Isles and may be equally at home in large towns or remote uplands.

It is slightly larger and more sturdily built than the rook, averaging about 100 g heavier and up to about 100 mm longer. There is much overlap between the two but the bill of the carrion crow is proportionately stouter and more adapted for tearing carrion than the more slender, digging bill of the rook. Wing span of the carrion crow is slightly broader than the rook's, and the former species tends to fly with slower wing beats. Again, as with the rook, females are on average slightly smaller than males.

The adult carrion crow's plumage is all black with a

greener iridescence than that of the rook. Juveniles are duller with no iridescence. The feathers of the tarsi are sleeker than those of the rook. The bill and legs are black and the eye is dark brown. The oldest carrion crow on record lived to be 13.5 years old, and expected lifespan is probably slightly less than the rook's (Busse 1969, Holyoak 1971, Hickling 1983).

In Britain carrion crows are non-migratory. Unlike rooks they are territorial. The area defended varies between 14 and 49 ha but may be larger outside the breeding season (Wittenberg 1968). They tend to be territorial (but not always) outside the breeding season but in winter flocks may form, although these are usually made up of non-breeding birds. In the breeding season they roost in the territory but at other times roost outside it. In winter they may roost singly or may do so communally with perhaps several hundred other carrion crows and many more rooks, jackdaws or ravens C. corax. Occasionally during the breeding season a third bird on the territory is tolerated by the owners of the territory. Although this bird may cooperate in the defence of the territory (Charles 1972) there is no evidence to suggest that cooperative breeding occurs.

The nest, usually placed in a tree, is built by both sexes and later than in the rook, normally in about the second week of March. Between late March and May a single clutch of usually 3 to 5 eggs is laid, with extremes of 1 and 7 on record (Holyoak 1967). Average clutch size, increasing with higher altitude, latitude and territory quality, has been observed to be as low as 3.4 eggs to as high as 4.7 eggs (hooded crow in Sweden, Loman 1977). In Britain Holyoak (1967) noted mean clutch sizes of 3.6 eggs in the south of England, 4.5 eggs in north England and north Scotland, and 4.0 eggs in Wales. As in most European passerines clutch size increases with increasing latitude (Holyoak 1967). Incubation, starting after the

laying of the second egg, is carried out by the female and lasts about 19 days. Approximately 90% of eggs hatch, although less do in late clutches. The male feeds the female and nestlings at the nest for about 10 days, after which he is helped by the female. Young fledge one month after hatching and normally only two or three nestlings from nests which reach this stage survive this period. Predation by humans and other crows accounts for many losses at both egg and nestling stages of breeding. Juveniles continue to be fed by their parents up to four weeks after leaving the nest. Mortality of young carrion crows is lower than that of young rooks and is fairly constant (at just less than 10%) in all months up to spring of their second calendar year when it almost doubles (Holyoak 1971). They may form flocks in winter and usually breed for the first time in their third calendar year of life, although many will do so in their second and some will not do so until their fourth.

The carrion crow selects almost any type of habitat in Britain - from uplands and moors to coasts and towns - providing that suitable nest sites are present. It is omnivorous and the range of items it consumes overlaps broadly with that of the rook and other corvids although the respective quantities of the various foods differ. The carrion crow eats less vegetable and more animal matter than the rook. The animal content of its diet includes many of the invertebrates favoured by rooks and also vertebrates. Invertebrates are less often taken from the subsoil than they are by the other species. Meat may be taken as carrion, for example dead hares and sheep, or the birds may prey on small mammals such as voles, mice and even rabbits. The vegetable part of carrion crow intake is made up mainly of grain but a wide spectrum of seeds and fruit is eaten. Food scraps are often scavenged for near human habitations.

More detailed, general accounts of the biology of these two

species may be found in Goodwin (1976) and Coombs (1978).

Chapter 2. The decline of the rook population of Britain

INTRODUCTION

It is often important in field studies to know the size of the population of animals whose biology is being studied. Even when the unit of study is not the population itself, for example in purely ethological studies, this may still be the case; so if an investigation focuses on the behaviour of individuals in their natural habitat but does not explore the relationships between those individuals and their habitat then an important dimension could be missing insofar as a complete understanding of their behaviour is concerned. Ways in which behaviour may be governed or modified by such ecological considerations are many and diverse. For example, the nature and evolutionary significance of many aspects of kittiwake, Rissa tridactyla, behaviour, including ritualised displays, are made more comprehensible with knowledge of its breeding ecology, specifically of the fact that it nests on cliff ledges unlike other gulls (Cullen 1957). Similarly, the complexity and meaning of the dance of honeybees, Apis mellifera, cannot be appreciated without knowing something about the distribution of the bees' food supply (Gould 1976). Population size is also an important part of the ecology of species and may also have (usually indirect) influences on behaviour. For example, at high population densities certain great tits Parus major may be forced to adopt poor quality territories, while at low densities birds which may not even have had a territory at all (and therefore would not have bred) may be enabled to acquire a good quality territory (Krebs 1971). Improved breeding success of these great tits may be seen as a consequence of their monitoring of the available habitat. The importance of population

density in governing reproductive strategy is such that selection may have favoured the evolution of complex song repertoires by great tits. By using these the birds may attempt to simulate high breeding density (i.e. by suggesting the presence of many birds) in order to prevent intrusions on to their territories (Krebs 1977). So while breeding density in this species may be limited by territorial behaviour aspects of the behaviour of poor quality territory holders or even non-territory holders is regulated by breeding density. A similar situation exists with the red grouse Lagopus lagopus (see e.g. Watson 1977). Ultimately, however, it is likely to be the quality and quantity of the food supply which governs the behaviour of territory and non-territory holders. If breeding population density in a species is so high as to result in severe competition for nest sites, leading to high mortality of young birds, then selection could result in the evolution of delayed maturation in that species (Orians 1969). Behaviour cannot be said to be adaptive until its ecology is understood: in this respect it is no different from morphology.

As well as complementing behavioural studies the study of the population ecology of species is valuable in its own right. This is particularly true of species which are, or are potentially, of economic importance to man. In cases where a species could be a pest an important first step in assessing the extent of the problem is to estimate the population size of the species. Only after having done this can one go on to investigate factors responsible for population growth and decline, and thereafter perhaps model the species' population dynamics. Such an approach is necessary for future effective control of a pest species (or, indeed, conservation of an endangered one). Not only is the number of individuals comprising a population important in this respect, but so is the way these

individuals are distributed in the environment, and thus the role the environment plays in governing the species dispersion. Measured over a number of years these parameters may provide approximate indications of other aspects of species biology such as productivity, the role of social factors in determining dispersion, demographic structure, migration rates, etc., although, of course, these would usually be measured directly. Estimates of population size taken over many years also highlight short and long term trends, and so facilitate the recognition of ecological and environmental determinants of population size. They also provide a sound foundation on which to build future research.

The above comments apply to the rook as much as they do to any other species of animal. This chapter is a review of investigations into rook populations, with particular reference to the decline that has occurred in the British population this century. Possible reasons for this decline are explored. The chapter which follows this one treats the rook population of N.E. Fife in more detail.

National surveys

The consequences of being at war made it imperative that Britain increased the production of home-grown food in the 1940's. With the resultant changes in farmland use it was important to know if the rook could be responsible for crop losses. In 1943 the Ministry of Agriculture and Fisheries therefore asked the British Trust for Ornithology, via the Agricultural Research Council, to assess whether the rook population of Great Britain had increased to a significant extent, and also whether the bird's feeding habits had changed. The ensuing survey, carried out mostly by amateur ornithologists, was conducted during the years 1943-1946 (mainly in

1945). Northern Ireland was not included in the survey and about two thirds of England, Scotland and Wales were censused. Although there had been many local surveys of rook populations prior to this (most notably that in Somerset, Tucker 1935) this represented the first attempt at estimating the size of the British rook population as a whole. The results of this survey indicated that the total number of breeding rooks in the country was around three million - 1,847,500 in England, 782,000 in Scotland and 196,500 in Wales. This represented an increase in the population size since the 1930's of about 20% (Fisher 1947). Although a higher proportion of grain seemed to have been taken by rooks than previously, no action aimed at widespread control of the species was recommended (Fisher 1948).

In 1975 the B.T.O. carried out another national rookeries survey. This time 94.3% of the U.K. was covered (including N. Ireland). The number of breeding birds was estimated to be 1,822,642, distributed as follows: England - 1,022,446 (a decrease since 1945 of 44.7%); Scotland - 504,678 (a decrease of 35.5%); Wales - 77,832 (a decrease of 60.4%); N. Ireland - 217,674; and a further 12 birds in the Channel Islands. In England, Scotland and Wales the estimated average decrease between 1945 and 1975 was thus 43.2%. The numbers used here are from Sage & Vernon (1978), but Castle's (1977) estimates for certain 10 km grid squares in Scotland have been used.

The B.T.O. followed this (almost) complete national rookeries survey with a sample census in 1980. The results of this indicated an increase in the number of nests in the five years from 1975 to 1980 of 6.8% (although the number of rookeries decreased by 7.7%). The largest increases occurred in the west of England (Morgan, Sage & Vernon 1981; B.L. Sage, personal communication).

Local surveys

In addition to these national surveys many local ones have been carried out throughout Britain. For the purposes of summarising the results of some of these the United Kingdom has been divided into several areas as shown in Figure 2.1 (pp. 40-41). These areas have been defined to make any geographical factors involved in population fluctuations more apparent. Area 1 includes that part of the country south of approximate latitude 52° N. Area 2 comprises mainland Britain north of 52° N and south of approximately 53° 30′ N. Area 3 is made up of the counties north of 53° 30′ N and south of approximately 55° N, and includes N. Ireland. Area 4 is those parts of Scotland and England north of 55° N and south of approximately 56° 30′ N. Area 5 includes all of Scotland north of 56° 30′ N, including the Orkney and Shetland Isles. Each of these five areas has been further divided into a western and eastern part, so defining ten areas in all. The old counties which make up each of these ten areas are given in the legend to Figure 2.1 (pp. 40-41). They will each be considered separately.

Area 1 (west)

There have been many rookery surveys in this part of the country this century. A few data are also available for the latter part of the 19th century up to the 1930′s, though these only for one large rookery. Along with another single, large rookery the trend up to the 1930′s was one of decline. Up to 1931 these two rookeries decreased in size by 59% and 45% from 1890 and 1909 respectively. It is not known whether these rookeries were representative of the area as a whole. During the late 1920′s and early 1930′s decreases in the range 23-35% were recorded in some localities, with a small increase of 2.5% occurring in part of Oxfordshire. From around this time up

to the 1945 national census the rook population seemed to grow, with increases of between 6% and 25% being noted in four areas. From 1945 up to the time of the second national census, 1975, all localities for which data have been published showed that the numbers of breeding rook had declined. These decreases ranged from about 7% to as much as 64%, in keeping with the trend in the country as a whole (see above).

In the late 1940's increases were noted in two districts, that in the Patney area of Wiltshire being described as "amazing". The West Gloucestershire population increased from 1933 to a peak in 1956, but declined by 23% from then until the mid 1970's. The indications are, then, that the large reductions in the rook populations of Area 1W took place in the 1950's, when decreases since 1945 in parts of the region were of the order of 40% (although part of Gloucestershire showed an increase of 22%). The decline continued into the early 1960's (the same part of Gloucestershire being no exception) and, somewhat less dramatically, thereafter. During the 1970's there were comparatively small fluctuations in population sizes.

Sources: Alexander (1933), Cawkwell (1950), Coombs (1961a), Cross (1950), Fisher (1948), Griffiths & Griffiths (1964), Harrisson (1931), Henry (1955), Nicholson & Nicholson (1930), Sage & Vernon (1978), Simson (1977), Tucker (1935), Vernon (1976), Wynne (1932), Yapp (1934, 1951).

Area 1 (east)

This region shows more or less similar trends to Area 1W with respect to changes in the sizes of its rook populations.

Whereas an increase of 26% in the population of part of

Sussex was recorded between 1939 and 1949, a decline of about 67% was noted in part of Buckinghamshire from 1932 to 1949. A decrease also took place in Middlesex between the 1930's and 1940's. Between 1945 and 1975 decreases of 60-70% took place in those populations in the eastern part of the region (e.g. Sussex, Kent), while increases of a smaller magnitude (up to 30%) were evident in western parts (e.g. Hertfordshire, Thames Valley). The greater increase between 1945 and the 1960's in Hertfordshire (84% overall) was also emphasised to have taken place in the west of that county. However, the Hertfordshire population had fallen to 45% of its 1960's level by 1975. In Middlesex there was a 20% increase between the 1940's and the 1950's (so returning to 1930's levels) but after this and up to the 1970's a dramatic crash in population size occurred, with there being very few rooks left breeding in the area. In another eastern county, Essex, there was a decrease of 65% between the 1950's and 1960's but there was a slight recovery thereafter to leave the 1975 population at about 47% of the 1950's size. Part of Buckinghamshire suffered a 20% reduction in the number of breeding rooks between the late 1950's and early 1960's. In part of Surrey there was a 90% decrease between the 1930's and 1970's and further reductions in the county during the 1970's.

The overall pattern in Area 1E seems to be similar to that in Area 1W except that the population in the eastern part of Area 1E appears to have declined much more than the one in the western part, which may have actually increased between 1945 and 1975.

Sources: Anonymous (1950), Ashby et al (1947), Darlington (1956), Harrisson (1953), Keen (1961), Moxey (1970), Parker (1970), Parker (1968), Pickess (1961, 1967), Sage (1972, 1976), Sage & Cornelius (1977), Sage & Nau (1963), Sage & Vernon (1978), Spittle (1948,

1949).

Taken as a whole the changes in the rook population of Area 1 show a general increase from the 1930's to the 1950/60's followed by considerable decline up to the 1970's. The pattern in the early 1970's was still one of decline, although there were small increases in some localities.

Area 2 (west)

Data from fewer localities than the previous areas are available for this one. However, two parts of Cheshire have been particularly well covered from the 1940's to the 1960's. From 1929 to 1944 there was a reduction in the rook population of the Wirral, Cheshire, of about 10%. This dropped a further 17% in the following year. From the 1947 level (which was 73% of that in 1944) the population size remained fairly stable but reached another peak in 1952 when it stood at 87% of the 1944 size. However, between 1952 and 1961 the number of nests counted decreased by 48%. Further decline resulted in the 1968 population standing at merely 39% of what it was in 1944. The situation in that part of west Cheshire adjacent to the Wirral was similar with a gradual decline from 1945 to 1965 of 68%. The period of greatest decline here appeared to be the late 1950's/early 1960's. The change in the Wirral population up to the 1940's was mirrored in part of Denbighshire where there was a 20% decrease in rook numbers between the 1930's and 1940's.

Between 1939 and 1944 rook numbers in one small locality of Shropshire declined by 29%. In Derbyshire, the population increased from 1929 to 1944 by 52%, but then decreased by 22% up to 1965/66. In fact the population here had grown up to 1958 so an even greater decrease must have taken place between 1958 and 1965/66. The census

for the same area in 1975 showed a further decline since 1965/66 of 23% (a total of 40% decrease since 1945). Between 1945 and 1965/66 there was a slight tendency for eastern and southern parts of the county to show the greatest reductions, and, in fact, increases in the north and west were recorded. During the 1970's a decline of 27% was noted in a smaller part of Derbyshire.

In some parts of Wales little change was noted between the late 1950's/early 1960's and 1975, but the population of Anglesey decreased between 1963/64 and 1966 by 11% only to return to the same level by 1975. This latter increase was also evident in Caernarvon where there was a 18% increase between 1966 and 1975.

The overall pattern in this area, as far as can be judged, is slightly different to that in Areas 1W and 1E. After decline up to the 1940's there was an increase in rook numbers from then up to the late 1950's and early 1960's. While this was followed by decline continuing up to and during the 1970's mainly in eastern parts of the area, population growth seems to have taken place in western parts.

Sources: Dobbs (1969), Henderson (1946, 1953, 1965, 1968), Lloyd (1939, 1940, 1949), Lomas (1968), Marples (1932), Roebuck (1933), Sage & Vernon (1978).

Area 2 (east)

The rookeries of this area have been well covered by surveys over the years.

Data from several whole counties show that their respective rook populations were increasing between the late 1920's and early 1930's to the time of the national survey in the mid 1940's (increases of between 45% and 74%, with only Lincolnshire showing a 2% decrease). This increase continued through the 1950's, but for a

small area of Suffolk which began to show decline in the early 1950's. By the early 1960's, however, widespread decline in rook numbers became apparent. In a short period between the late 1950's and early 1960's decreases of 38% and 67% were noted, with overall reductions since 1944/45 ranging between 11% and 74%. Only the Nottinghamshire population remained at the same level in 1962 as it was in 1944 but the 1962 population had nevertheless declined by 38% from 1958. From the late 1960's to 1975 decreases (ranging from 8% to 49%) were still taking place in the counties for which data are published. During the 1970's the limited amount of data available suggest that rook numbers stabilised in this period.

Sources: Beverley & Hickling (1965), Dobbs (1964, 1969), Easy (1964, 1965, 1966), Jeans & Snook (1976), Roebuck (1933), Sage & Vernon (1978), Tebutt (1969).

The pattern in Area 2 as a whole is thus quite similar to that noted for Area 1. The rook population of most of the area seemed to increase from the late 1920's/early 1930's up to the the late 1950's and to decline from then, with perhaps some levelling off in the 1970's. The situation in the extreme west of that area, however, appeared to be different. Here the population did not begin to expand until the 1940's and while a decrease took place in the late 1950's/early 1960's the sizes of rook populations probably increased between the mid 1960's and mid 1970's.

Area 3 (west)

The part of England included in this area is a small one and consequently there are few published reports of rookery surveys for it. The same is true of N. Ireland. Only for the Isle of Man

and parts of Lancashire have the results of repeat surveys been published.

In the Isle of Man the rook population increased during the years between the two world wars. From 1938 until 1945 there were small annual fluctuations in rook numbers (ranging from -8% to +8%) but with little change over this period as a whole. From 1945 to 1975, however, there was a 20% decrease.

In part of Lancashire from 1928 to 1940 there was a 4% decrease in population size with annual changes again being small (apart from a 30% decline from 1928 to 1929). In other parts of N.W. Lancashire there were reductions of 36% from the 1950's to 1960's and of 53% from the 1960's to 1970's. In E. Lancashire, though, there was an increase of 35% during the 1960's followed by a further small increase into the early 1970's. During the 1970's the N.W. Lancashire population increased by 26% while that in the eastern part of the county decreased by 12%.

Sources: Flintoff, Green & Ward (1940), Green & Flintoff (1939), Holdsworth (1962), Sage & Vernon (1978), Williamson & Cowin (1940, 1942, 1945).

Area 3 (east)

This area has been very poorly covered by local rookery surveys. Data from only two repeat censuses have been published.

In the Leeds area the rook population increased from 1945 to 1955 by 12%, and in the Doncaster vicinity there was a decrease of 13% from 1964 to 1975.

Sources: Jackson (1959), Sage & Vernon (1978).

It is difficult to summarise the trends in population size for Area 3 as a whole due to the lack of published reports. Most of the area does show a similar pattern to that in other areas (see above). This is one of population growth up to the 1950's followed by decline continuing into the 1970's. In central parts of the area, however, growth seemed to prevail up to the early 1970's after which there was decline, while populations in extreme western parts of the British mainland increased in the 1970's, this being similar to the situation found in Area 2.

Area 4 (west)

Most of the data available for this area also show the trend in rook populations this century to be one of decline.

In Lanarkshire the rook population increased by 26% between 1922 and 1929. Part of this population, that in Glasgow, had increased by 151% from 1900 to 1935. Nest counts from a sample of 28 rookeries in the city suggest, however, that the population may have been declining towards the end of this period as the 1935 level stood at only 50% of the 1929 level (which had, like Lanarkshire as a whole, increased by 20% since 1922). A single well-studied rookery in the city showed great fluctuations in numbers of nests between 1912 and 1946, increasing overall by 53% during this time, and by 13% between 1936 and 1946.

In western parts of nearby Dunbartonshire a 10% reduction in numbers took place between 1922 and 1929. From then the population size fell by over 80% (perhaps as much as 90%) up to 1975. In other parts of this county there was a 14% decrease between the 1940's and 1975, and in the Loch Lomond area a 20% decrease in the same period. Still in the western part of the region the rook population of Ayrshire decreased by 31% from 1956 to 1966, and

recovered slightly (by 8%) by 1975.

Further east, in Stirlingshire as a whole, there was little difference between the number of nests counted in 1945 and 1975. In Dumfriesshire, again in the eastern part of Area 4W, the population decreased by 9% from 1908 to 1921. Population size increased by 6% up to 1963 and rose again the following year. After comparatively slight reductions in each of the next two years the population increased again, and in 1975 stood at a level 25% greater than it was in 1963.

From 1975 to 1980 increases were noted in some localities, notably in the Loch Lomond area (up 21%).

Sources: Castle (1968, 1977), Dennis (1981), Graham (1937), Mitchell (1976), Rennie (1937, 1949), Sage & Vernon (1978), Skilling et al (1966), Stewart (1923, 1930), Walls (1956), Watt (1900).

Area 4 (east)

Apart from the city of Edinburgh no repeat counts of rookeries were made in this area between 1945 and 1975. There are also few data available prior to the 1945 census. Some of the largest declines in rook populations between the times of the two national surveys took place in this area.

Of the seven Scottish counties for which data have been published six of them showed decreases between 1945 and 1975 which were greater than the average decrease for Scotland as a whole of 40.6%. Decreases of under 50% were recorded for Kinross and W. Lothian, of over 60% for Berwick and Midlothian, and of over 70% for Roxburgh and Fife. The decline in N.E. Fife was slightly greater than in W. Fife (76% vs. 68%). Rook numbers in E. Lothian dropped by 27% in the thirty years up to 1975. The Berwickshire population was

about the same size in the 1940's as it was in 1887. Part of Midlothian contained more nests in 1928 than did the whole county in 1975, but it is not clear if there was an increase here between 1928 and 1945.

Rookeries in Edinburgh have been particularly well studied. Between 1886 and 1921 there was a decrease in rook numbers of around 70% in part of the city. After 1921 the population in the whole city grew to almost double its size by 1935, but fell to 19% of this by 1944. Between this date and 1957 there were no large changes in population size, but between 1957 and 1964 there was a 51% decrease and this dropped a further 31% up to 1970. The trend in the 1970's was still one of decline (-8% between 1970 and 1975), but the population of Midlothian did increase by 11% between 1975 and 1981.

Sources: Alexander (1933), Dennis (1982), Evans (1921), MacMillan (1957), Munro (1970b), Nash (1928, 1929), Sage & Vernon (1978).

Generally, rook populations in Area 4 have been declining this century, with those in eastern parts showing the most marked decreases. Some populations in the west and south of the area seem to have been increasing, but there is no clear geographical pattern discernible in the available data.

Area 5 (west)

Very little data pertaining to this area has been published, partly because rooks have never been as common here as elsewhere. In Sutherland the population increased by 41% from the mid 1940's to 1975. Rook nests numbered "well over 200" in 1939 near Stornoway on the Isle of Lewis. In 1970 there were about 250. This decreased to 190 in 1972. Subsequent counts produced the following

results: 1973 - 195 nests, 1975 - 212, 1979 - 178, 1981 - 180. So this population (albeit only four rookeries) has remained fairly stable throughout the past forty years.

Sources: Castle (1977), Dennis (1971, 1973, 1974, 1980, 1982), Nicholson (1951), Sage & Vernon (1978).

Area 5 (east)

Rooks are more numerous in the east of Area 5 and consequently more data on the various populations are available. This area also includes Aberdeenshire where rooks have been the subjects of long term investigations, and where the largest rookery in Britain exists (over 6,000 nests in 1945).

There was a general trend for populations in the south of this area to exhibit greater decline between the 1940's and 1975. Thus, the Kincardineshire and Angus populations were reduced by 47% and 35% respectively during this time. The corresponding decreases for Aberdeenshire and Banff were 19% and 25%. Populations in the extreme north actually increased in this period. In Caithness rook numbers showed a substantial increase from the 1920's to 1945, increased by about 6% up to 1971 and increased again by about the same amount from then up to 1975. The Orkney Islands population, also having increased from the 1920's to 1940's, increased further by 64% up to 1975 and has continued to grow (by 41%) into the 1980's. The Shetland Islands were first colonised by rooks in 1952 with 9 nests and reached a peak of 176 nests in 1973 although this fell to 110 nests by 1975.

The intensively studied rook population of the River Ythan valley in Aberdeenshire increased markedly from 1963 to 1966 and has remained more or less at the same level in the 1980's.

Sources: Adam & Corse (1983), Dennis (1972, 1979, 1982), Dunnet & Patterson (1965), Richardson et al (1979), Sage & Vernon (1978), Venables (1973), Watson (1967).

There is a clear indication in Area 5 that from 1945 to 1975 decreases in the region were less than in other areas, while in the four northernmost counties increases actually occurred. Virtually nothing is known, however, of trends in population levels from 1945 to the early 1960's other than the fact that rooks established themselves on the Shetland Islands.

DISCUSSION

It must be remembered that the summaries presented above for each area are sometimes based on few data, and that therefore the trends which have been highlighted may not be real ones. There are many areas where counts of rook nests were not made between 1945 and 1975 and some results refer, as indicated, to single rookeries. There will inevitably be errors involved in estimating the size of rook populations, especially when repeat counts have been made by different observers. Notwithstanding these comments, a clear pattern emerges from the results of the rookery surveys summarised above. They show that in most counties rook populations decreased from 1945 to 1975. Furthermore, it is likely that most of them increased up to the late 1950's/early 1960's, after which the widespread decline began. Rook numbers appear to have stabilised in the 1970's. There is some evidence to suggest that the reductions in the sizes of rook populations in extreme western parts of Britain was less than that in more easterly areas, and also that recovery in the 1970's was more marked in these western localities. There is clearer evidence that populations in the extreme north of the country have been growing

this century.

Many possible reasons have been put forward to explain the large decline of the breeding rook population of Britain between 1945 and 1975. These include control by shooting, increasing urbanisation, the effects of bad weather, the destruction of elm trees by Dutch elm disease, the use of pesticides and changes in agricultural practices.

Shooting. The shooting of rooks was once a common method of attempted control of the species (and also a form of sport). Typically, young rooks were shot after they had left the nest but not the rookery, i.e. when they were perched on branches near their nests. Females were also shot as they sat on nests incubating. Shooting is not so common nowadays but it is still done on a very local basis throughout the country. The effectiveness of shooting in controlling rook populations in Britain seems to have been minimal. Although whole rookeries have been exterminated large reduction in numbers seems not to have been achieved. Despite intensive shooting at one locality in Hertfordshire from 1945 to 1961 the breeding population increased over this period (Sage & Nau 1963, Sage 1972). This illustrates that shooting was ineffective perhaps because it led to reduced competition among the surviving breeders, so increasing their chances of survival to subsequent breeding seasons, or, more likely, that the number of birds breeding in subsequent years had been boosted by immigrants to the area. This example shows that what is necessary for lasting and effective control is shooting carried out intensively over long periods of time and, more importantly, over widespread areas, in conjunction with other control methods. In the Netherlands there was a 20% decline in the rook population between 1944 and 1970. This was due mainly to a widespread campaign of

control which, besides shooting, included poisoning and disturbance of nests (Feijen 1976). No such organised campaign of this magnitude has ever been planned or executed in Britain. It is thus extremely unlikely that shooting was the cause of the decline of the British rook population between 1945 and 1975.

Urbanisation. Local rook populations certainly do decline or even become extinct as a result of land being claimed for building or for industry. In a part of Cheshire and in a Welsh valley, for instance, the decline of rook populations in the post-war period was attributed to such developments (Henderson 1968, Griffiths & Griffiths 1964). Sage (1972) reported data for nest counts in the vicinity of urban areas in Hertfordshire for 1960/61 and 1971 and stated that increasing urbanisation had had an adverse effect on rook numbers. The rook populations of these urban areas declined by 43% during this period. This compared to a decrease of 32% for the county as a whole, so it is difficult to state categorically that urbanisation was the cause of the decline here. It probably had local effects but is unlikely to have caused such wholesale decline, especially as the area of agricultural land increased in the same period (Sage 1972). Rook populations in cities have also been shown to diminish in size as these cities grow, for example in Edinburgh (MacMillan 1957). Many authors have pointed out, however, that urbanisation seems to affect the rook but little (e.g. Holdsworth 1962), and this makes sense provided that flight to feeding grounds from the rookery is not made energetically inefficient and that little human disturbance of rooks occurs. If these do become problems then rooks may desert the rookery. What is most likely to result if urbanisation prevents rooks from nesting in established rookeries is a redistribution of these rooks, not their extinction, so that, all other things being

equal, increases in areas surrounding urban developments should become apparent. This was found to be the case in Edinburgh (MacMillan 1957). It is unlikely that urbanisation is anything but a minor factor responsible for the diminution of rook numbers, and certainly it cannot account for the large scale decline in question.

Weather. The approximate time when the rook in Britain apparently began to show widespread decline coincided with one of the harshest winters of this century - in 1962/63. Young rooks, especially those encountering their first winter, are sensitive to changes in the weather, and suffer greater mortality at this time than older birds while otherwise their monthly mortality patterns are similar (Holyoak 1971). This results, at least in part, from the fact that young birds with less fat reserves and less food in their gizzards occupy less favourable (i.e. more exposed) positions within the winter roost (Swingland 1977). Despite this, the severity of the 1962/63 winter appeared to affect the rook (and other corvids) very little (Dobinson & Richards 1964), and so this cannot be held responsible for the decreases in rook populations which took place at about that time.

Sage & Vernon (1978) suggested that climatic variation could be linked with fluctuations in rook numbers. They noted that increases in British rook populations were accompanied by a process of climatic amelioration in the 1930's and 1940's, and that decreases in the 1960's were accompanied by a reversal of this, leading to cooler springs and wetter summers. However, such a relationship must remain at most tenuous and at least speculative. Feare et al (1974) found that the period of greatest food shortage for rooks was the summer. This was due to increased food requirements coupled with reduced availability of sub-soil invertebrates. As the ground gets harder because of dry weather rooks find it more difficult to capture

items such as earthworms and leatherjackets, Tipula spp., which burrow deeper in hot, dry conditions. Wetter summers, then, would make these prey more available to rooks and might therefore lead to increased survival. So far, no relationship has been established between long term fluctuations in rook numbers and meteorological variables. Annual fluctuations, though, could be a consequence of weather conditions affecting the availability of the food supply.

Dutch elm disease. Although this disease was first recorded in Britain in the 1920's it was only from 1969 that it led to destruction of elm trees on a large scale. Up to 1978 almost 11 million trees were infected and 5 million had already been felled (Osborne 1982). Most of the damage took place in the very south of the country. Sage (1972) and Sage & Vernon (1978) stated that such loss would affect rook numbers and distribution, especially as over one quarter of rook nests in 1975 were built in elms. Some counties had over 60% of their nests in elm. As with urbanisation, though, redistribution rather than extinction of rooks should occur, as rooks are adaptable and may nest in a wide variety of tree species. In fact the 1975 rookeries survey showed that more nests were built in beech and Scots pine than in elm, although in England the latter species was the most important. That rooks do nest in other trees if elms become unavailable or unsuitable was suggested in Hampshire where after felling of an elm tree rookery two new rookeries (one of them in elms again however) were founded the following year and containing almost the same number of nests as the old rookery (Simson 1977); and in West Gloucestershire where from 1972 to 1975 nests in elm trees decreased by 28% while nests in ash trees showed a concomitant 19% increase (Vernon 1976). Conceivably, if rooks did nest or roost in dead elms (which would therefore be defoliated) then

they might be more vulnerable to lower temperatures and high winds, but this would not result in the large decreases in populations, especially where elms were comparatively unimportant for these purposes. As mentioned, the disease affects mainly the south of Britain yet the large decline of the rook population took place over almost the entire country. Reviewing some of the effects of Dutch elm disease on wild birds Osborne (1982) concluded that the disease had very little effect on rooks. Tapper (1981) also showed that the loss of elm trees occurred much later than the decrease in rook numbers in East Anglia, and suggested that if elm disease had had any effect on the rook population then it had been to retard its recovery. Much the same case may be made for the effects of the felling of trees in general. Only a redistribution of rooks should result unless felling is so widespread as to prevent the birds from nesting anywhere at all, which is unlikely for several reasons.

Pesticides. It is of interest that the widespread and increased use of organo-chlorine insecticides coincided with the decline of the British rook population. Following the second world war DDT was used extensively on farmland to control many insect pests. Perhaps more striking, as far as the decline of the rook (late 1950's/early 1960's) is concerned, was the use of certain organo-chlorine insecticides of the cyclodiene group. These were introduced in 1955 but their use was restricted in 1962. They included dieldrin and aldrin (which converts in time to dieldrin), and they were used, amongst other ways, as seed dressing on wheat in order to control wheat bulb fly. These chemicals are very effective insecticides. They are also very stable and accumulate in the bodies of animals which ingest them directly or via animal prey or carrion. A strong relationship was established between organo-chlorine poisoning and

bird mortality which led to a ban on the use of cyclodienes as dressing on spring sown grain in 1962, and an almost total ban on their use in 1965 (Moore 1965). In the late 1950's thousands of birds, particularly seed-eaters, were found dead or dying in cereal growing areas where dieldrin had been used as a seed-dressing (Mellanby 1967). Although pigeons, Columba spp., were the main victims many rooks were also found dead in fields and below rookeries. Dobbs (1964) suggestively linked rook deaths in Nottinghamshire in the springs of 1960 and 1961 to seed-dressings. Less anecdotally, organo-chlorine residues were later found to be present in many bird corpses, including those of rooks (Cramp et al 1964). Levels of residues present in rook bodies (and in one egg) were very small and not considered to be sufficient to categorically implicate organo-chlorine seed-dressings as the cause of mortality (Moore 1965). Even in 1974, however, rooks were reported to have been affected by dieldrin (Cooke 1979).

Being at the top of the food chain some birds of prey suffered the most serious reductions in numbers as a result of organo-chlorine pollution. As corvids generally are at a high trophic level they might be at greater risk than many other species. Common prey for corvids (and also for some species lower in the food chain) are beetles, slugs and earthworms. All of these have been discovered to carry varying amounts of organo-chlorine residues so the dangers to rooks are certainly not confined to the ingestion of dressed seed dug up from the soil.

Ratcliffe (1970) drew attention to the inverse correlation between levels of organo-chlorine residues in birds and the thickness (or relative weight) of their eggshells. This probably contributed to the cause of egg breakages in many raptors which were reported at the time. He also found that after the introduction of

organo-chlorine insecticides the thickness of rook eggshells diminished by a significant factor of 5% (and of 4.8% for carrion crow eggshells). Reviewing the situation in raptors, Newton (1979) lucidly implicated DDT (or rather its very stable metabolite, DDE) in eggshell thinning and cyclodiene compounds in mortality.

While no proof exists, it is clear that organo-chlorine poisoning, perhaps acting in conjunction with other factors, could have been a major cause of population decline in the rook. The timing and location of events provide much circumstantial evidence for this:

the greatest use of organo-chlorine pesticides was in the farmland of eastern Britain - the areas where rook populations have declined most;

the period of their most intensive use was the late 1950's and early 1960's - the time when the rook seems to have shown the greatest reduction in numbers;

recovery and growth of the British rook population has been greater in northern and western areas - the areas where pesticide use was least prevalent. (The sparrowhawk, Accipiter nisus, one of the raptors affected very badly by organo-chlorine poisoning, also showed greatest recovery in northwestern areas of Britain when the use of these insecticides was restricted - Newton 1979).

It is worth noting here that Cooke (1979) also suggestively linked the decline of the magpie in parts of England with the use of cyclodiene compounds.

Where the rook is beginning or is continuing to recover then the latency of this recovery is not surprising given the chemical stability of the chemicals involved. However, organo-chlorines cannot be causally linked with rook mortality or

eggshell thinning as unfortunately the necessary analyses of corpses and eggs were not done at the time.

In part of Sweden, Malmberg (1973) reported a 54% decrease in rook numbers between 1955 and 1965 which was quickly followed by increase. In the period of recovery low to moderate levels of organo-chlorine residues were found in rook tissues. During the period of decline, however, high levels of mercury were discovered in rook corpses. This was almost certainly the cause of much rook mortality, having been ingested by rooks via grain which had been dressed not only with alkylmercury fungicide but also with aldrin. It might be the case that this combination of aldrin and mercury is more harmful than either substance on its own. Most cereal seed in Britain is also treated with mercury compounds but again there is no evidence to suggest that this had a deleterious effect on rooks in the 1950´s and 1960´s. It could be significant that the mercurial fungicide used in Sweden was ethyl or methyl based whereas that used in Britain at the time was phenyl based (Mellanby 1967, Malmberg 1973).

While the evidence against pesticide use is suggestive as a cause of the decline of British rook populations it is circumstantial, and so the case must remain unproved.

Agricultural practices. The changes made in the use of land consequent upon the second world war were many and, for the most part, lasting. Intensive farming methods with their increased emphasis on mechanisation came to stay. The effects these had on rook numbers are difficult to gauge and once again only retrospective guesses can be made.

Modern cereal farming means, of course, that harvesting and threshing are carried out by the same machine in the fields. This

has resulted in the disappearance of stooks of grain left standing in the fields after harvesting. Stooks were formerly exploited by rooks which, if necessary, opened them in order to feed on the grain. Harvesting by combine harvesters has also probably resulted in less grain being spilled during the harvesting process - grain which would once have been available to rooks for feeding. So it is possible that a reduced amount of vegetable food is available to rooks at certain times of the year than was available thirty or forty years ago.

Apart from intensive methods of farming the greatest changes in agriculture witnessed since the war have been in the way the land has been used. In the 1930´s much land was not tilled as there were no pressing demands for food to be home-grown. Over 7.5 million ha were devoted to permanent grassland (Stamp 1955). With the onset of war much of this was ploughed up to accommodate various crops. By 1950 about 3 million ha of it had been given over to arable crops. Some land was reclaimed by permanent stands of grass by the late 1960´s and from then up to the present day about 5 million ha of permanent grassland has remained (O.E.C.D. 1974, Mellanby 1981). Since the 1950´s and 1960´s much land has been used for temporary grass leys - roughly the same amount as permanent grassland was lost. An important invertebrate food supply for rooks is earthworms and it is old, permanent grassland which supports the highest populations of these (Mellanby 1981). Modern direct drilling of cereal seed at the time of sowing also results in reduced availability of invertebrates as fewer of these are left exposed on the surface by this method (Mellanby 1981). So again, important components of rook diet seem to be less available now than during the 1930´s.

Of the permanent grassland ploughed up before and during

the war many hectares were used for the cultivation of cereals. The area of land under wheat, for example, was almost six times as much in 1943 as it was in 1931 (Stamp 1955). In the 1950's more or less equal areas of land were used for growing oats, barley and wheat, with that for the latter being about half of what it was in 1943. Since the 1950's, however, there has been a gradual decline in the area of land used for oats. The acreage of wheat has remained at about the same level (in 1977) as it was after the war, although with a temporarily reduced acreage in the 1960's (Stamp 1955, O.E.C.D. 1974, Mellanby 1981). Yields from these crops have, of course, increased greatly since the war. The area of land used for the production of barley has grown enormously since the 1930's. In 1977 more than twice the area of land under wheat was under barley (O.E.C.D. 1974). With improved autumn sown varieties becoming available the area of land used for this cereal is likely to continue to increase.

Notwithstanding the reduction in the availability of certain foods due to the ploughing up of permanent grassland it seems that more grain in the form of spillage left in stubble fields should result from an increase in cereal growing. Rooks should be able to exploit this grain, but any increased availability of grain is difficult to quantify, and is complicated by the fact that in some localities stubble is burned very soon after the cereal has been harvested, thus making no spilled grain available for rooks. The nature of this presumed increased availability of grain may also be important. Rooks are known to prefer wheat (and oats) to barley (Luniak 1977), so not only the amount, but also the quality, or efficiency of exploitation, of the grain may be significant factors as far as rook feeding habits are concerned.

If we assume that rook numbers have been affected by

changes in the food supply due to changed patterns of land use then the most likely way in which this has happened is via nestling mortality. If an increased amount of grain has become available over the years then the time when the birds would benefit from this is after the breeding season, i.e. at harvesting time in late summer and also in the autumn. If the availability of the rook's invertebrate prey has been lowered due to the ploughing up of old grassland then this is most likely to have an effect during the breeding season - when nestlings require for growth the protein that invertebrate prey provide. Adult rooks also require invertebrates at this time, and shortly after the breeding season they may be an important food source when the birds are moulting.

Many authors have attempted to explain fluctuations in the sizes of their local rook populations with reference to land use patterns. Sage (1972) stated that there was no clear relationship between rook numbers and acreages of cereals or grass in Hertfordshire, while others have anecdotally linked declining rook numbers with decreased areas of land used for cereal growing (e.g. Yapp 1951, Sage & Nau 1963, Easy 1965, Castle 1968, Henderson 1968, Lomas 1968). Dobbs (1964) was of the opinion that rook numbers were correlated with grain acreage until the introduction of organo-chlorine pesticides. Few authors have statistically tested for any possible relationship between land use and rook population levels, but Castle (in Sage & Vernon 1978) found a significant negative correlation between population size and the area of land termed rough grazings in Scotland from 1945 to 1975, and also a significant positive correlation with the area of land under grass. Sage & Vernon (1978) found that no similar correlations existed in England but that in Wales rook numbers were correlated with grassland acreage. Roebuck (1933) reported rook numbers in seven parts of the

Midlands (mainly whole counties) and also gave some data on land use. A close look at his figures reveals a highly significant positive correlation between rook population sizes and the total area of land under arable crops and grass ($r = 0.970$, 5 df, $p < 0.001$). Further analysis shows that the relationship between rook numbers and arable land area is significant ($r = 0.787$, 5 df, $p < 0.05$), while that between rook numbers and area under grass just fails to be significant ($r = 0.678$, 5 df, $p < 0.1$).

While much of the above confirms that rook biology is closely linked to patterns of land use and with agricultural activity in general, it must be stressed that the evidence for implicating changed farming practices in the decline of the rook in Britain is slender. It is possible that changes in rook food availability at crucial times of the year which have been contingent upon changes in land use and farming methods has contributed to the reduction in rook numbers.

The causes of the decline would be better understood if more exhaustive treatment of the (admittedly few) data were made. What is required is an approach which attempts to examine the contribution of several factors, each acting independently and also in conjunction with others. Although simple partial correlation methods help in this respect few authors have attempted even this, while others have been content to merely make anecdotal statements about the reasons for rook population decline. Even with few data (many areas were not surveyed between 1945 and 1975) a more analytical approach is possible and could prove rewarding. Such an approach is applied in the next chapter to the N.E. Fife rook population.

While the reasons for the decline of the British rook population are not known for certain, this review suggests that it

was something to do with the changes in farming that followed the second world war. Probably both the more intensive and efficient use of the land and the introduction of harmful pesticides contributed to the decline, while other potential causes were of lesser importance. We cannot rule out the possibility that unknown factors were responsible, however, so the populations of rooks in Britain should be closely monitored.

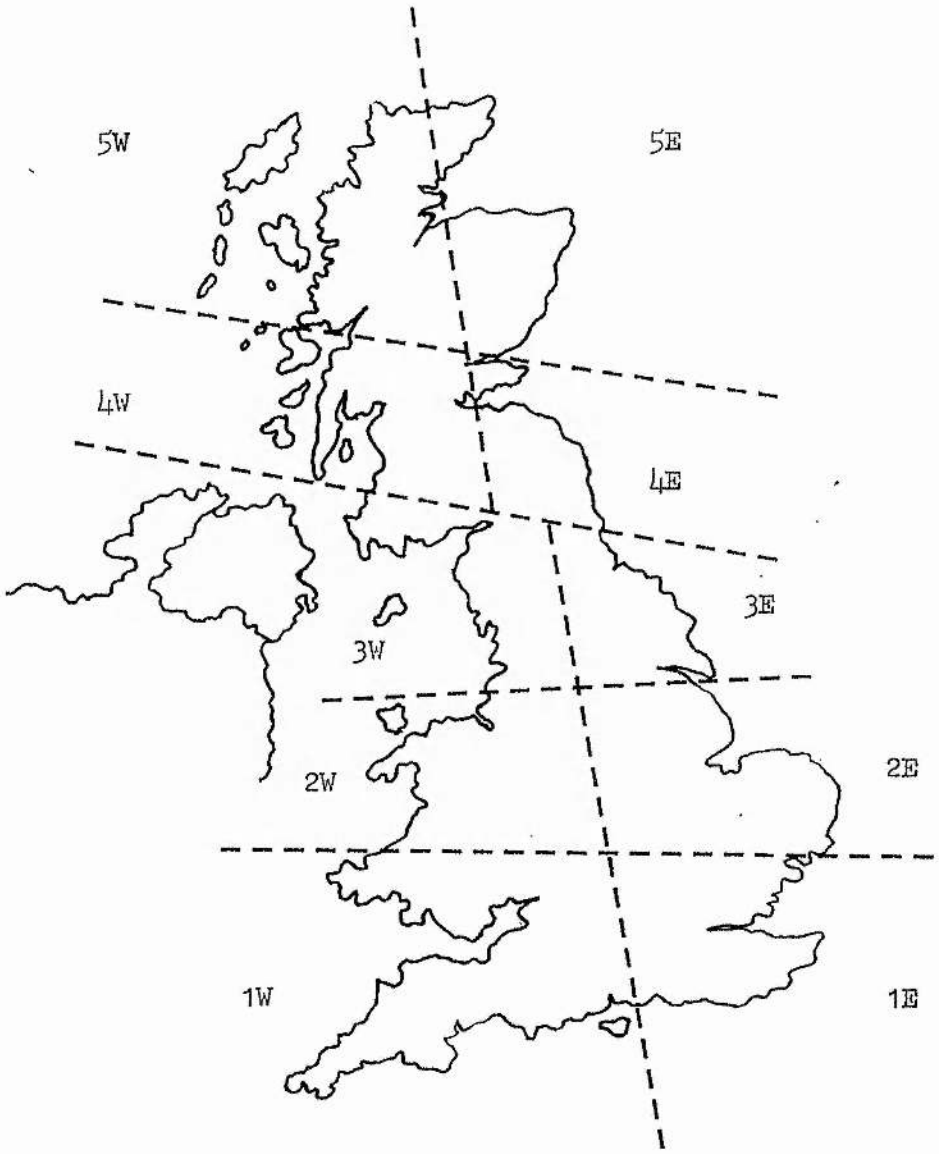


Fig. 2.1. Map showing the areas into which the U.K. was divided for summarising trends in the sizes of rook populations. Old counties included in each area are as follows:

Area 1W - Cornwall, Devon, Somerset, Dorset, Gloucester, Wiltshire, Hampshire, Berkshire, Oxford, Pembroke, Carmarthen, Brecon, Monmouth, Glamorgan, Isle of Wight.

Area 1E - Buckinghamshire, Hertfordshire, Middlesex, London, Surrey, Sussex, Kent, Essex.

Figure 2.1 (continued)

Area 2W - Cardigan, Radnor, Montgomery, Merioneth, Caernarvon, Anglesey, Denbigh, Flint, Cheshire, Salop, Herefordshire, Worcestershire, Staffordshire, Warwickshire, Derbyshire.

Area 2E - Leicestershire, Northamptonshire, Rutland, Nottinghamshire, Lincolnshire, Bedfordshire, Cambridgeshire, Huntingdonshire, Norfolk, Suffolk.

Area 3W - All N. Ireland, Isle of Man, Lancashire, Cumberland, Westmorland, Wigtown, Kirkcudbright.

Area 3E - Durham, Yorkshire.

Area 4W - Ayrshire, Dumfriesshire, Renfrewshire, Bute, Lanarkshire, Argyllshire, Stirlingshire, Dunbartonshire, islands south of Tiree and Coll.

Area 4E - Northumberland, Roxburgh, Berwickshire, Selkirk, Peebleshire, West Lothian, East Lothian, Midlothian, Fife, Kinross, Clackmannan, Perthshire.

Area 5W - Invernesshire, Ross & Cromarty, Skye, Outer Hebrides, Sutherland.

Area 5E - Angus, Kincardineshire, Aberdeenshire, Banffshire, Morayshire, Nairn, Caithness, Orkney Isles, Shetland Isles.

Chapter 3. The rook population of N.E. Fife

INTRODUCTION

Johnston (1923) reported nest counts of rookeries in parts of Fife but only mentioned the existence (in 1921) of five in N.E. Fife. All of these were located in the vicinity of the town of Cupar. Only two of them (those at Tarvit and Lochmalony) existed for certain twenty-four years later when the national survey of rookeries was carried out. Between these dates (1921 and 1945) no census of rookeries took place in N.E. Fife but Grierson (1962) referred to four rookeries in the area which existed in 1960. These were at Earlshall ("over 500 pairs"), Guardbridge, Tayport and Leuchars. The first two of these were in existence in 1945 and continue to be so up to the present, while the other two are now extinct.

The returns for the 1945 survey were made by L.J. Rintoul and E.V. Baxter. These two workers provided with the returns much background information on Fife rookeries, including the age of some of them. Of the nine rookeries which Rintoul and Baxter reported as being less than 10 years old in 1945 seven are now extinct; both rookeries which were between 10 and 20 years old in 1945 are now extinct; of the three which were between 20 and 50 years old one is extinct; and of the seven which were greater than 50 years old five are now extinct. In addition, of three rookeries which were described as "many years old" two are extinct and of seven described as "old" four are extinct. Most of the rookeries which were counted in the 1975 national survey were still in existence in 1978 and later.

A total of 14,466 nests in 83 rookeries was counted in N.E. Fife in 1945. In 1975 the corresponding figures were 3,452 nests in

77 rookeries. Ostensibly, this represents a 76.14% decrease in the number of breeding rooks in the area over a thirty year period. However, many problems are associated with the counting of rook nests, and these may be especially significant with regard to national surveys. The most obvious problem is that when many people are involved in the surveying of a large area many rookeries may not be counted at all. For anything like complete coverage to be attained it is preferable that the survey be done by people (or even one person) who know the area well in terms of the location of rookeries. Even when an area is well-known one can never be sure if all rookery sites have been recorded. In 1945 Fife was, as mentioned, censused by Rintoul and Baxter. These were arguably the most distinguished ornithologists in Scotland at the time, and their writings give the impression of great attention to detail. For these reasons the 1945 rookeries census in Fife was probably as near complete as one could hope for. The 1975 census in N.E. Fife, on the other hand, was carried out by almost a dozen people. This resulted in some rookeries being missed so the figure of 3,452 nests counted in that year must only be taken as a very rough approximation. The number of rookeries omitted was unlikely to have been so great as to disguise the fact that there had been a large decrease in the rook population since 1945.

METHODS

For convenience, each rookery recorded in N.E. Fife in the 1975 national rookeries survey was given a reference number. This consists of two digits followed by a / followed by another two digits. The first two two digits indicate the Ordnance Survey 1:25 000 NO sheet on which the rookery is located. The second pair of digits identify the rookery as number 1, 2, 3, etc. and these were

applied randomly. Thus the rookery at Crail Church (Grid Reference NO 614080) was given the reference number 60/03, indicating that it was the third rookery to be assigned a reference number in sheet NO 60. Any subsequent rookeries discovered in the area covered by this sheet would be assigned the reference numbers 60/04, then 60/05, and so on.

Censuses of the N.E. Fife rookeries were made in 1977, 1978 and 1979. Those in 1977 and 1979 were sample censuses, only the nests in some rookeries being counted. In 1978 an almost complete census was made. In addition, complete (or, again, almost complete) censuses were carried out in 1980 and in 1983 but the results of these, while they may occasionally be alluded to, for the most part lie outwith the scope of the present study.

The method of estimating the size of the breeding population of rooks in a defined area is fairly straightforward, but there are several sources of error of which the researcher must be aware in order that the results obtained be as accurate as possible. Errors may be of many kinds. Perhaps the most serious type is that of not counting the nests in a rookery at all. This may happen because the locations of all rookeries in the study area are not known. Searches for unrecorded rookeries, while they may be intensive, will probably never result in all rookeries being discovered in a single season. To overcome this problem one must draw on local knowledge, but there is no substitute for getting to know the area thoroughly oneself and this takes years. Although as complete coverage of the study area as possible was attempted in the 1978 survey several rookeries which almost certainly existed were missed. A related problem here is that "rookeries" containing only a single rook nest are even more difficult to locate. (These are referred to as being rookeries in the present study). Such nests

might be very transitory, being occupied for only one season, and so pass undiscovered. If they form the genesis for new colonies then these may be discovered in subsequent years but it remains that the survey results for one year will be inaccurate. This inaccuracy is unlikely to be of great magnitude, however. There is a danger also that solitary carrion crow nests may be counted as rook nests but this should not be a problem (and was not in this study) as verification of the species is just a matter of waiting and observing.

A second class of problems which might lead to error in estimating rook population size concerns the nests. Just what constitutes a rook nest may be far from clear. Nest structures in rookeries at the time of counting can be of four general types:

1) a well-formed structure, solidly built, which would clearly accommodate one rook plus brood;

2) a vertical mass of twigs up to several feet tall;

3) a laterally sprawling mass of nest material which could have room for several pairs of rooks to nest in; and

4) a less solid structure having the appearance of a partly built nest which might eventually be used for nesting by one pair of rooks.

Structures of type 2 are a consequence of birds building a nest using the nest(s) of a previous year as a foundation. Those of type 3 probably result from this as well but also from birds building nests so close together that a large platform is gradually created. Type 4 structures are in all likelihood partly built nests. It is equally likely that they will be eventually completed or remain unfinished. They may be the first attempts at nest building by young rooks (Nau 1960) or they could be renewed attempts at constructing a nest by adults.

In the surveys all structures of type 1 were counted as one

nest (equivalent to two breeding birds). Nests of type 2 were also counted as one. Type 3 structures presented more problems. If discrete nests were at all obvious within these then each was counted as one. This was occasionally an easy judgment to make as the shapes of individual nests could be observed by changing one's angle of view from the ground. If strips of daylight were discernible through these conglomerations then this also served as a criterion for counting more than one nest. In some instances it was not possible using these standards to separate the large mass of nesting material into individual nests. In these cases a somewhat arbitrary definition of the number of nests they contained was used. This was the maximum number of nests that could be contained if each nest was 1 m apart from any other nest in the structure. Such a definition is unlikely to lead to gross errors in estimating the number of breeding pairs. Depending on its appearance a type 4 structure could either be counted as a nest or not. If no daylight was visible through the structure from any angle, thus suggesting that a nesting platform had been built, then it was counted as a nest. If daylight was discernible through it then it was not counted as a nest. Again there was room for error here but in most cases it would probably be of a magnitude of much less than 5% of the total count for a rookery.

These comments lead on to third category of possible inaccuracy in the estimation of the breeding population size. That is the question of whether all nests counted as such are in fact occupied by a breeding pair of rooks. With structures which have the appearance of being partly built nests it is difficult to ascertain whether these will be eventually used for breeding purposes. If young birds are responsible for building them then there is perhaps an even chance of this being so. It is possible that these constructions are the remnants of nests from the previous breeding

season, and so will not be used to rear young. The chances of this leading to a large margin of error are slight, however, as most nests (in deciduous trees at least) are destroyed by the elements after the breeding season, and also any nests which do survive until the following spring will either be used as foundations for new nests or will be dismantled for the material for new nests to be built elsewhere in the rookery. Roebuck (1933) suggested that adult pairs of rooks may build two nests in a season and only use one of them. Again this would not appear to be a serious problem in estimating breeding numbers. Unused nests would probably be quickly plundered for the material they contained, given that there is usually competition for this (Roskaft 1982).

The counting of nests in pine trees can be especially difficult. In particular, the problems just discussed concerning nest structures are exacerbated. In the present study the same criteria used to count nests in deciduous trees were used for coniferous ones but instead of looking for daylight through and between nests it was necessary to attempt to discern "spaces". For this reason there is perhaps a greater margin of error in nest counts made in coniferous trees but again it is unlikely to be greater than 5%, and probably much less - especially in small trees and small rookeries. It is also difficult (but not impossible) to discover previously unrecorded rookeries if they are built in coniferous trees as the nests may not be visible from even very short distances.

A problem in large, sprawling rookeries is keeping track of which nests have been counted and which have not. This is a matter of organization and memory, but if there was any doubt then the count was abandoned and started again.

The timing of a rookeries census is important. The time of the year when rooks begin to build their nests depends on several

exogenous factors, including daylength and temperature (see e.g. Busse 1965). The nest building period may be prolonged. The best time for counting nests is therefore as late as possible. This ensures that all nests built by adults will be counted, while very late nests built by inexperienced birds who will probably not breed will not be included in the count. In the present study all counts were made as late in the spring as was feasible, i.e. before leaf cover obscured nests in deciduous trees. This varied from late March to as late as mid May, but most counts were made in mid to late April each year.

The number of nests in every tree in each rookery was recorded on cassette tape using a hand held microrecorder. Binoculars (10x) were used when necessary. As well as number of nests, the species of tree in which these nests were contained was also recorded. This data was transcribed on to paper the same day and the date of counting noted. The geological substrate on which each rookery stood was obtained from the Ordnance Survey 1:63 360 (1 in to 1 mile) Geological Survey map for Fife. The altitude (to the nearest 25 feet above sea level) of each rookery was also ascertained using O.S. 1: 25 000 maps. A rookery was defined as one or more rook nests greater than 100 m distant from any other rook nest, the standard B.T.O. definition.

RESULTS

A list of N.E. Fife rookeries is given in Appendices I and II. These indicate the reference number of each rookery, its O.S. national grid map reference, the number of nests it contained in the years 1945, 1975, 1977, 1978 and 1979, its altitude, its geological substrate and the genera of trees in which the nests counted in 1978 were contained.

The 1977 and 1979 surveys

In 1977 a total of 23 rookery sites were surveyed. These were 30/06, 31/07, 31/09, 32/01, 32/03, 40/16, 41/03, 41/06, 41/11, 41/12, 42/02, 42/03, 42/04, 42/05, 50/01, 50/05, 50/07, 51/02, 51/05, 51/06, 60/01, 60/02 and 60/03. The total number of nests counted in these rookeries was 1,624. This compares with 1,422 nests counted in the same rookeries in the 1975 national rookeries survey. If this sample was representative of the population as a whole then it would indicate an increase in the population of 14.21% from 1975 to 1977. All but one of these rookeries (41/06) was counted in 1978 also, and these figures indicate a further increase from 1977 to 1978 of 7.18% (data for 41/06 excluded). Overall, from 1975 to 1978, an increase of 14.43% was suggested (again with 41/06 excluded).

In 1979 nests at 10 rookery sites were counted. These were 40/16, 41/01, 41/11, 41/12, 41/13, 41/14, 41/15, 50/01, 51/02 and 51/12. These totalled 340 nests. Data for nine of them were available for the years 1975 and 1978 (the omission being 51/12). The figures indicate an increase in these rookeries of 29.95% from 1975 to 1978, with a decrease of 13.67% from 1978 to 1979 (an overall increase of 12.18% from 1975 to 1979).

Data is available from a sample of 25 rookeries which pertain to the years of the main surveys, viz. 1945, 1975 and 1978. These rookeries are 30/03, 30/04, 30/12, 30/16, 31/01, 31/06, 31/07, 32/03, 40/01, 40/05, 40/06, 40/07, 40/10, 41/03, 41/05, 41/14, 42/04, 42/05, 50/03, 50/04, 50/05, 51/03, 51/05, 60/01 and 60/03. A total of 6,551 nests were counted in these rookeries in 1945, 1,334 in 1975 and 1,327 in 1978. These figures represent changes of -79.64% from 1945 to 1975 (-79.74% from 1945 to 1978) and of only -0.53% between 1975 and 1978. This pattern resembles more closely the pattern of change indicated by the results from all rookeries censused in these

years.

Due to the problems associated with estimating the sizes of rook populations (see above) these figures are not accurate, although they probably give a rough indication of trends. The following rookeries which almost certainly existed were not counted in the 1975 national rookeries survey: 32/04, 40/17, 40/18, 41/16, 51/07, 51/08, 51/09, 51/10, 51/11, 51/12 and 51/13. The following rookeries were not included in the 1978 survey: 31/02, 31/08, 41/06, 41/08, 41/09, 50/06, 51/04 and 51/13. Of these, 31/02 and 31/08 could not be found, a request for access to 41/06 was denied, 41/08, 50/06 and 51/04 were probably extinct and 51/13 was neither recorded nor discovered (although it certainly existed).

The 1978 survey

A total of 4,220 nests in 72 rookeries resulted from the 1978 survey. This represents a decrease since 1945 of 71.83% - a reduction of 10,246 nests, or over 20,000 breeding birds. The decline in numbers in Scotland from 1945 to 1975 was approximately 36%, in England 45% and in Wales 60%. In Fife as a whole there was a decline of 72.3% during this period (Sage & Vernon 1978).

The mean number of nests per rookery in 1978 was 58.61 (s.d. = 67.28). This compares with the average rookery size for Scotland as a whole in 1975 of 78.9 nests/rookery (including estimates for areas not surveyed, Castle 1977). Corresponding figures for England, Wales and N. Ireland were 24.4, 25.2 and 39.4 respectively (Sage & Vernon 1978). In Fife as a whole in 1975 a mean number of 49.7 nests/rookery was recorded (Castle 1977) and the value for N.E. Fife in 1945 was 174.29 nests/rookery (s.d. = 203.30).

The mean density of nests in the study area in 1978 was 8.10 per km^2 and therefore the mean density of breeding birds was

16.20 per km^2. The density in the whole of Fife region in 1975 was 5.66 nests/km^2 (Castle 1977). In 1975 the mean density of rook nests was 3.26 per km^2 in Scotland, 3.9 per km^2 in England, 1.9 per km^2 in Wales and 8.0 per km^2 in N. Ireland (Sage & Vernon 1978). In 1945 the density of nests in N.E. Fife was 27.77 per km^2. Although these figures are interesting for comparative purposes, they could be misleading because they refer to total land areas. Comparisons would be more meaningful if rook densities were expressed in terms of the area of suitable habitats available to the birds. This is extremely difficult to ascertain, however, given that rooks nest in a wide variety of locations, tree types and altitudes, and utilise an equally wide variety of feeding locations.

Table 3.1 (p. 85) shows the distribution of rookeries by size. The majority (38.89%) contained less than 25 nests while about an equal number of rookeries contained between 26 and 50, 51 and 100 and 101 and 200 nests (20.83-16.67%) and there were only three rookeries with over 200 nests (31/09, 41/03 and 50/05). The number of rookeries in the study area has remained fairly constant over the years (83 in 1945, 72 counted in 1978 but probably 78 in existence). The distribution by size of these rookeries in these two years differs markedly, however. In 1945 the majority, 20.48%, of rookeries were in the 26-50 nests category. This is about the same percentage as existed in 1978 (20.83%), but in 1945 only 19.28% of rookeries were in the 1-25 category compared to the majority of 38.89% in 1978. While only 1.39% (one rookery) contained over 301 nests in 1978, 21.68% (18 rookeries) did so in 1945 and, in fact, nine rookeries contained over 500 nests each in this year.

Table 3.2 (p. 85) shows the number of nests contained in rookeries of different size categories. Most nests (38.63%) were recorded in rookeries containing between 101 and 200 nests, with a slightly smaller number (24.29%) in rookeries in the 51-100 category. Fewest nests, not surprisingly, were recorded in the smallest size category (5.50%). The nine rookeries which each contained more than 500 nests in 1945 accounted for 40.05% of all nests. In that year only 1.14% of nests occurred in rookeries of 25 nests or less.

These comparisons show clearly that while the number of rookeries has not changed significantly over the 33 years from 1945

to 1978 the number of breeding birds has, and that there has been a tendency for rookeries to become smaller. Although many rookeries have become extinct since 1945, new ones have been founded. The trend is for these new ones to be smaller than 1945 rookeries and for rookeries still in existence since that date also to be smaller. Sage & Vernon (1978) also reported that since the 1940's and 1950's rook colonies in several parts of the country have become smaller.

The number of nests which were built in the various species (or rather genera) of trees is shown in Table 3.3 (p. 86). Just under half (48.91%) of all nests were recorded in coniferous trees (Gymnospermae), the great majority of these being Scots pine Pinus sylvestris. Of the nests found in broadleaved trees (Angiospermae) twice as many were in beech trees than in sycamore trees (26.82% vs. 13.10%). Other broadleaved trees were poorly represented, with only elm and oak registering greater than 1% of all nests. In 1975 Pinus trees also predominated as the most common type of tree in which rook nests in Scotland were found. Beech and sycamore were, as in this study, the two most common broadleaved trees. In England in 1975 most rook nests were found in elm trees, in Wales in oak trees and in N. Ireland in beech trees (Sage & Vernon 1978).

In 1945 the distribution of rook nests by tree species in N.E. Fife was quite different to that found in 1978. About the same number of nests were found in Pinus species in these two years, these being 2,251 in 1945 and 1,965 in 1978. The former figure represented only 15.56% of all nests, whereas in 1978 nests in pine were 46.56% of the total. In 1945 the most commonly used tree for nesting was sycamore (35.48% of all nests), followed by beech (28.15%) and then Scots pine. Most other species were comparatively unimportant, although elm contained 1,297 nests (8.97% of the total). Nine rookeries which existed in 1945 but were extinct in 1978 are known to

have been felled. The number of nests built in the various tree species in these rookeries were: sycamore - 485; beech - 422; horse chestnut - 154; lime (Tilia spp.) - 154; Scots pine - 149; elm - 136; spruce - 23; ash - 22; oak - 20; poplar (Populus spp.) - 8; larch - 2. These figures indicate that since 1945 felling of broadleaved trees has been more extensive than that of coniferous trees. Furthermore, the most commonly used trees for nesting by rooks in 1945 were those which have been felled to the greatest extent since then. This could account for the marked difference in the distribution of rook nests over tree species between 1945 and 1978.

Table 3.4 (p. 87) contains information on the distribution of rookeries with regard to altitude. Most (30.77%) were less than 100 ft above sea level, and there was little variance in the proportions contained in the other 100 ft interval categories (7.69-14.10%). The distribution in N.E. Fife was very similar to that found in Scotland as a whole (Castle 1977). However, there was a markedly greater proportion of rookeries in the 500-599 ft category in the present study (14.10%) than in the corresponding category in Castle's analysis (6.2%).

The average size of rookeries at various altitudes differed little, with the largest (94.88 nests, s.d. = 61.14, N = 8) being in the 200-299 ft category and the smallest (34.38 nests, s.d. = 51.37, N = 26) being less than or equal to 100 ft above sea level.

The number of rookeries standing on various geological formations is shown in Table 3.5 (p. 87). The majority (39.74%) were on calciferous sandstone. Of the others, only carboniferous limestone and dolerite underlay more than 10% of all rookeries. The average rookery size on the various formations differed widely with only 6 nests per rookery on coal measures (s.d. = 7.97, N = 5) but 116.71 nests per rookery on andesitic lavas (s.d. = 135.54, N = 7). Only one rookery accounted for the

figure of 122 nests per rookery on millstone grit.

These data on altitude and geology of rookeries are purely descriptive ones. They have little analytical value and for them to have any one would of course have to know the absolute areas of land in each altitude and geological substrate category in the study area. This would be difficult in the case of altitude but less so with geology for the appropriate statistical comparisons to be made. Though merely a common way of describing aspects of the distribution of rookeries, the data are presented for reasons of precedence and completeness.

The 1980 and 1983 surveys

In 1980 a total of 4,088 nests was counted in 66 rookeries. This represents an apparent decrease in the breeding population since 1978 of 3.13%. At least five and perhaps eight rookeries were not counted in this year, however. The corresponding figures for the 1983 survey were 5,471 nests in 67 rookeries. This, again ostensibly, represents an increase in the population since 1980 of 33.83% and since 1978 of 29.64%. All known rookery sites were visited in 1983.

Clearly, the N.E. Fife population of rooks is a typical one, certainly as far as other agricultural areas of Britain are concerned. This is evidenced by the fact that there was a large decrease in the number of breeding rooks in the area between 1945 and the 1970's. The decrease, of around 70%, compares with the average decrease in roughly the same period in Scotland of about 36%, and in Britain as a whole of about 43% (Sage & Vernon 1978). The only other county in Scotland, indeed in Britain, for which figures are available which showed a greater decrease than Fife (including W.

Fife) was Roxburgh. Possible reasons for this decline will be discussed later in this chapter.

Changes in the size of rookeries

The number of rookeries in N.E. Fife did not change markedly in the same period - the trend was for some rookeries to become extinct, some other old rookeries (i.e. those existing in 1945) to become smaller and for new rookeries (those founded after 1945) also to be smaller. As stated above, this trend was reported from other parts of Britain as well. Patterson et al (1971) showed that the high number of rooks in Aberdeenshire was a consequence of rookeries there being very large. It was not the case that there were many more smaller rookeries than in other areas of Britain. The reasons why rookeries were smaller in the 1970's than they were in 1945 are not clear. The genesis of rookery foundation between these dates is not known. Did the surviving birds in whole rookeries desert en masse to found new rookeries? Or has colony foundation been a pattern of growth from a comparatively smaller number of birds who emigrated from their natal colony? If so, were these birds established breeders or were they young birds attempting to breed for the first time? Such questions cannot be answered in this study. They would, of course, be difficult to investigate anyway, as the frequency of colony foundation is low, the location of new rookeries difficult to discover and the number of birds that would have to be individually marked to identify their rookery of origin would render the task of marking them impractical.

Apart from questions regarding the determinants of population size (for which see later in this chapter) one must attempt to discover what has governed the size of individual rookeries at particular points in time. The type of factors which

are important in this respect are, broadly, environmental and social ones. With regard to environmental factors the most important would seem to be the nature of the rookery in terms of its tree structure and its distance to feeding grounds. To the human eye there was little variation between many rookeries with reference to the extent of tree canopy, age/size of trees and general aspect. It would be useful to know the precise abundances of tree species in the study area in order to determine if the differential use rooks made of the various species can be accounted for in terms of the availability or abundances of these tree species. As felling continues to be carried out, however, and due to the difficulty of monitoring change, up to date information on the abundance of tree species is not available. However, rookeries appeared to exist in almost any type of wooded position except, that is, in the middle of very large woods. The number of different tree species (and therefore the branch structure within rookeries) used for nesting by rooks in this study, and in others, testifies to what would appear to be indifference in the choice of nesting site. The numbers of nests in the various trees probably reflects the relative abundance of these trees. Furthermore, as N.E. Fife is intensively arable and little built-up no rookeries are more than 300-400 m distant, at the very most, from farmland - even those in towns. The effect of social factors in determining rookery size are largely unknown. Richardson et al (1979) reported that breeding adults established in one rookery tend not to move to other rookeries to breed. Therefore, it is the behaviour of young rooks, particularly their choice of rookery in which to breed, which will govern the growth or otherwise of a rookery. The origin of birds breeding in a rookery for the first time has been little studied but Dunnet & Patterson (1968) showed that the growth of some rookeries could not be accounted for by the

numbers of nestlings hatched in those rookeries. Richardson et al (1979) demonstrated that not all young rooks returned to their natal rookery to breed and Grace (1973) reported that the recruitment of young rooks to a breeding colony was not associated with their origin. So the question of what makes one rookery more attractive than another to a young rook for breeding remains open - it is not a simple case of young returning to the rookery in which they were hatched (although some do). Nor is it known if all young rooks behave similarly with respect to their preferred choice of a breeding rookery. A detailed investigation of the many environmental and social factors involved in the selection of a breeding rookery is outwith the scope of this study but an attempt was made to identify the contribution of some factors important in governing rookery size.

In a stepwise multiple regression analysis the following independent variables were entered in order to discover how much variance in the size in 1978 of 25 individual rookeries (dependent variable) they could explain: the altitude of each rookery (x_1), the number of nests each rookery contained in 1945 (x_2) and the distance of each rookery to its nearest neighbour (x_3). The 25 rookeries used in this analysis were those for which census data were available for each of the three years 1945, 1975 and 1978 (see above). The data are shown in Table 3.6 (p. 88). Multiple regression is a technique for obtaining the best prediction equation for a dependent variable using several independent variables. It is of the form

$$y = a + \sum_{i=1}^{N} b_i x_i$$

where y is the dependent variable

x_i are the independent variables

N is the number of independent variables

a is the intercept of the line (a constant)

and b is the regression coefficient of each independent variable (i.e. the amount by which each independent variable must be weighted for optimal linear prediction of the dependent variable)

The multiple correlation coefficient (R) is the correlation between the predicted (derived from the above equation) and the actual values over all observations of the dependent variable. The proportion of variance in the dependent variable which is accounted for by the independent variables is given by R^2. The overall significance of the regression is tested using analysis of variance.

The equation $y = -23.98 + 0.01x_1 + 0.13x_2 + 28.03x_3$ accounts significantly for 39.32% of the variation in rookery size in 1978 ($F = 4.54$, 3,21 df, $p < 0.01$). Two variables, number of nests in 1945 (x_2) and distance to nearest rookery (x_3) were significant ($t = 2.42$, 21 df, $p < 0.05$ and $t = 3.04$, 21 df, $p < 0.01$ respectively) and accounted for 39.29% of the variation in 1978 rookery size. Of those used, then, the best predictor of a rookery's size in 1978 was its size in 1945. Its altitude was not a good predictor of its size. Its distance to the nearest rookery was also a good predictor of its size. The relationship between rookery size in 1945 and 1978 suggests that over a comparatively long time span there are usually only slight fluctuations in colony sizes. This is not to deny that rookeries may become extinct or may expand greatly in shorter or longer time spans, of course. Felling of trees in a rookery could cause either, as perhaps could social factors.

Dispersion of rookeries

It is interesting that there was an association between the distance from the nearest rookery and rookery size (correlation coefficient, $r = 0.46$, 23 df, $p < 0.05$). As this association was positive it suggests that large rookeries tend not to

be close to other, smaller rookeries. The reasons for this could be environmental - for instance it could arise because of a shortage of suitable rookery sites in parts of the environment so that rooks are obliged to form large rookeries on the available sites. Or perhaps young rooks may find one particular rookery in the area especially attractive and so adopt it as a breeding rookery, this eventually leading to extinction of other rookeries in the vicinity. Dunnet & Patterson (1968) also noted that large rookeries tended to be further from their neighbours than small ones in the Ythan Valley, Aberdeenshire. Again, whether the reasons young rooks find a particular rookery more attractive than others are environmental or social cannot be stated.

The geographical distribution of rookeries in 1978 is depicted in Fig. 3.1 (p. 113). To test if this distribution was random or otherwise it was compared with a Poisson distribution (Pielou 1969). The study area of N.E. Fife was divided into 1 km^2 quadrats. Only those quadrats which contained at least 25% land were included for the purposes of analysis and those which contained only coastal marsh, sand or rock were not included. The reason for these stipulations was in order that those quadrats which were clearly unsuitable for rooks to nest in be excluded from analysis. The number of quadrats containing 0, 1, 2, etc. rookeries was then ascertained and the resulting distribution compared with the expected distribution derived using the terms in a Poisson series. The Poisson series dictates that the expected proportion of quadrats containing r rookeries will be $m^r e^{-m}/r!$, where m is the observed mean number of rookeries per quadrat. So the expected proportion of quadrats containing no rookeries is e^{-m}, one rookery me^{-m}, two rookeries $m^2e^{-m}/2$, three rookeries $m^3e^{-m}/6$ and four rookeries $m^4e^{-m}/24$. The mean and variance of the Poisson distribution are

equal, indicating randomness. If the mean of the observed distribution exceeds its variance then the subjects of study (organisms usually, but in the present case rookeries) are said to be uniformly distributed. If the variance exceeds the mean then the subjects of study are said to be clumped or aggregated. Statistical comparison of the observed and expected distributions is made using the chi square test.

The observed and expected numbers of quadrats containing differing numbers of rookeries in 1978 in N.E. Fife were thus:

Quadrats containing	Observed	Expected
0 rookeries	624	613.171
1 rookery	52	68.825
2 rookeries	6	3.863
3 rookeries	3	0.145
4 rookeries	1	0.004

The requirements of the chi square test are that fewer than 20% of cells must have an expected frequency of less than 5 and that no cell has an expected frequency of less than 1 (Siegel 1956). As the data here violate these conditions the last three categories were combined. This still means that more than 20% of the cells have an expected value of less than 5, and so the resulting chi square value will be inflated. Nevertheless, the test was carried out in order to obtain a rough indication of the nature of the distribution of rookeries, and in any case the chi square test is an extremely robust one (Snedecor & Cochrane 1956). The result was $X^2 = 13.25$. With df = 1 the probability associated with this chi square value is $p < 0.001$. As the variance exceeds the mean one may tentatively conclude that rookeries in 1978 were aggregated. There were certainly more

quadrats than expected containing no rookeries and fewer than expected containing one rookery, with the consequence that more quadrats than expected contained 2, 3 and 4 rookeries.

The geographical distribution of rookeries in 1945 is shown in Fig. 3.2 (p. 114). The 1945 rookeries survey data were subjected to a similar analysis. The corresponding observed and expected numbers of quadrats containing differing numbers of rookeries were:

Quadrats containing	Observed	Expected
0 rookeries	614	607.832
1 rookery	65	73.542
2 rookeries	4	4.449
3 rookeries	2	0.179
4 rookeries	1	0.005

Again with the last three categories combined, $X^2 = 2.26$, 1 df, $0.2 > p > 0.1$. As any error produced by more than 20% of cells having an expected frequency of less than 5 would not be conservative then one may safely conclude that rookeries in 1945 were not significantly aggregated. Although the distributions from the two years do not significantly differ from each other these analyses suggest that rookeries may have become closer together from 1945 to 1978.

Between 1945 and 1978, then, rookeries in N.E. Fife became smaller and probably more clustered. Larger rookeries also became further from these clusters of smaller rookeries. This pattern almost certainly resulted from the fact that there was such a large decline in rook numbers in this period. As the decline took place many rookeries became extinct. There are indications that the rook

population in Britain (see chapter 2) and in N.E. Fife (results of post 1975 surveys) entered a phase of recovery in the late 1970's. As new (and therefore small) rookeries were founded after the decline there could have been a tendency for these to fragment into other small rookeries close to the parent rookery. This could account for the diminished size of rookeries and also for their clumped distribution.

Sociology of the rookery

A tentative explanation for the fact that old, large rookeries became more isolated is that their smaller neighbours became extinct during the period of decline while they, the larger rookeries, did not as they were more stable. They may have been more stable because of 1) the large number of rooks they contained and 2) a tendency for birds not to break away from the parent rookery. Why should the rooks in small rookeries have been more liable to desert their rookery than those in larger ones? Again the reasons may have been social. Perhaps large rookeries are more attractive to rooks for nesting in than smaller ones and Richardson et al (1979) have made a strong case for this. But one must ask here why rooks nest in colonies at all. The answers to this have not been fully elucidated.

Large rookeries may be more attractive as a result of the Fraser Darling effect. Darling (1938, 1952) suggested that colonial breeding may provide "social stimulation" necessary for successful reproduction. He showed this to be so in the herring gull Larus argentatus, and suggested that for many species a certain number of breeding neighbours was essential for breeding success. Below this threshold breeding attempts would be largely unsuccessful. This effect has been shown to operate in several species of colonial breeders, mainly seabirds but also in passerines (for examples see

Wilson, 1975). A likely mechanism whereby success can be achieved is that of breeding synchrony. This means that young mature at the same time, so leaving potential predators with a glut of vulnerable prey as opposed to a steady supply. The role of the social stimulation which colonially breeding birds receive in enhancing spermatogenesis and ovulation may also be important but seems to have been studied little in birds.

Another possible reason why rooks nest in colonies is that potential predators of eggs, young or adults are more easily located and deterred by a large group of birds than by single birds or smaller groups. For example, Powell (1974) showed that captive groups of ten starlings Sturnus vulgaris detected and reacted to a model hawk more quickly than single starlings, and Kenward (1978) reported similar results from observations on wild woodpigeons Columba palumbus which were approached by a goshawk Accipiter gentilis.

A third possible function of colonial breeding in rooks is that it may enable them to exploit their food supply more efficiently. This may come about in two ways. Rooks which on one day have not fed as well as others in the rookery may follow these well-fed birds to feeding grounds either during the day or in the morning as the day's foraging begins. So far, there is no evidence for the rookery being used in this way as an "information-centre" (Ward & Zahavi 1973), although Feare et al (1974) anecdotally suggested that it might and Loman & Tamm (1980) showed that hooded crows and ravens in Sweden might use roosts as such. There is good evidence, however, showing that rooks are more likely to land on a field if there are already foraging rooks on that field, and also that while on a field individual rooks can increase their prey intake by being attracted to other foraging rooks within the field (Waite

1981). As existing proximity to other rooks would facilitate the operation of local enhancement mechanisms for finding feeding grounds and food patches the concentration of birds into breeding colonies may indeed be a consequence of the pressure on rooks to exploit resources as efficiently as possible. The rookery may then be used as a base from which to find other rooks (and therefore food patches) more easily. At first sight it should seem that if rookeries were founded close to grass fields (which are especially important for rooks in the summer - see chapter 4) then colonial breeding would not be of any particular advantage in locating these fields. However, in the breeding season rooks tend to feed further from the rookery than they do in autumn and winter (Patterson et al 1971). The locations of grass fields may change from year to year as well, of course. Environmental considerations could nevertheless be important in the selection of a rookery site.

If a small rookery is unattractive to nesting rooks because of its reduced potential to provide the above benefits it may be to the advantage of these birds to attempt to nest in a large, established rookery. If there are risks in gaining acceptance into, or close to, such a rookery, however, then birds may attempt to breed at a new rookery site which is close to an existing small rookery and where the opportunities for local enhancement to food patches might still exist, if not those for social stimulation and predator detection.

It must be stressed that despite intensive studies of rook ecology and behaviour the mechanisms responsible for colony growth and extinction, rookery site selection and the choice of young rooks of a rookery in which to breed are poorly understood. Notwithstanding Grace (1973) and Richardson et al (1979) the exact emigration rates of young rooks from their natal colony have not been

quantified. Nor have the immigration rates of young rooks to breeding colonies of various sizes and distances from the natal rookery. Such data could be essential for a complete understanding of the above problems. Consider the following. Individuals who exploit resources more efficiently than, or compete more favourably with, their conspecifics will hold a selective advantage over them in terms of survival, breeding or both. While the selfish interests of the individual would seem to be paramount in these respects the nature or intensity of competitive interactions with conspecifics might be thought to vary depending on the amount of genetic material they share by common descent (Hamilton 1963). The inclusive fitness of an individual is important, then, this being measured not only by the success of that individual but also by the success of those genes in other individuals which are identical to those in the individual in question. Thus altruistic, or at least seemingly tolerative behaviour, in various animals (for example Hymenoptera - Hamilton 1972, lions - Bertram 1976) may be understood by recourse to kin selection arguments. Parental care is perhaps the most striking example. Usually, kin selection may be considered as a possible explanation for apparently altruistic acts if the advantages to the recipient of an act outweigh the costs to the actor or donor by a factor greater than the reciprocal of the degree of relatedness between donor and recipient. The important prerequisite for altruism, however, is that there be a positive regression of the recipient's genotype on the donor's genotype. Hamilton (1975) thus stated that kinship may only be one way of obtaining this positive regression and so the concept of inclusive fitness is more wide ranging than that of kin selection (see also Dawkins 1979). So the beneficiary of an altruistic act need not be close kin of the altruist.

Hamilton (1975) speculated that in a species whose population is divided up into relatively closed groups (i.e. one with low inter-group migration) average coefficients of relatedness between individuals within groups will become greater than those between individuals from different groups. In other words there will exist a larger positive regression coefficient of a potential recipient's genotype on a potential donor's if both recipient and donor belong to the same group than if they belong to different groups. So we should expect there to be less overt competition between same-group members than between different-group members, other things being equal. Of course, within group competition will persist and will be at the same level in all groups irrespective of size, varying only with the numbers of animals migrating to and from them. Dawkins (1979) pointed out that this formulation highlights altruism as a relative concept and should lead to "strong xenophobia".

The importance of quantifying the degree of natal dispersal and adoption by young rooks of a rookery in which to breed is apparent. If young rooks tend to return to their natal rookery to breed then each member of a rookery will tend to have a high average coefficient of relatedness with other members. On the other hand, if they do not return to their natal colony to breed then rookery members will be as equally related to each other as they will be to members of other rookeries. As mentioned, young rooks may or may not return to their natal rookery, and hence coefficients of relatedness between same-rookery and different-rookery individuals cannot be gauged unless the dispersal patterns of young rooks are known. Once these have been assessed over many years colony growth and extinction will become more understandable. Although rooks from different rookeries do not seem to have exclusive feeding grounds, Patterson et

al (1971) did find that different groups of rookeries tended to have separate feeding grounds. Rooks from these different groups of rookeries mixed little. If degrees of relatedness are important in rook sociality then perhaps selection has acted to produce semi-isolated breeding groups, with individuals showing tolerance towards members of their own group and a degree of xenophobia towards members of other groups. Such a scenario could help in explaining some aspects of rook behaviour but begs some questions also. Future studies of rook social organization could be rewarding if approached from this angle.

Factors affecting the decline of the N.E. Fife population

The possible reasons for the decline of the British rook population which were outlined in the previous chapter will now be discussed with respect to the N.E. Fife population. The effects of the weather, or changes in the climate, though, will not be touched on as these are difficult to assess for an area as small as N.E. Fife. In the light of comments in chapter 2 the precise consequences of short or long term climatic variation on rook populations are poorly understood.

Shooting. For the reasons discussed in chapter 2 this has probably had little or no effect on rook numbers in N.E. Fife since the second world war. Smith (1952) stated that most rookeries in Fife were shot in the late 1940's (providing, incidentally, a source of food for the human population), but Rintoul and Baxter, in their 1945 census returns, mentioned only for a few rookeries that shooting took place. Some rookeries in the study area are still shot, evidenced by small numbers of empty shotgun cartridges, and occasionally corpses (see chapter 6), found on the ground below rookeries. There are no

indications, however, that this is done either on a large scale or a regular basis.

Urbanisation. N.E. Fife was mainly rural in character in 1945 and has remained so up to the present day. There will have only been a negligible effect at most of urbanisation on rook numbers as little urbanisation has occurred. Similarly, industrialisation will not have affected rooks as there is little heavy industry in the area. West Fife is more densely populated and industrialised than N.E. Fife and the growth of industry and the human population was greater between 1945 and 1975 in W. Fife. Yet the decline of the rook population between these years was slightly less in west than in north-east Fife (67.71% compared to 76.14%).

There is a suggestion that human activity has had an impact on rook numbers in the vicinity of R.A.F. Leuchars air base, north-west of St. Andrews. Within a 2.5 km radius of the base there existed, in 1975 and 1978, eight rookeries. These were 41/01, 41/02, 41/05, 41/14, 42/02, 42/03, 42/04 and 42/05. The numbers of nests these rookeries contained in the two years compared with all other rookeries in N.E. Fife were as follows:

	1975	1978
Leuchars	480	292
Others	2972	3928

Quite apart from the large difference between the two years the number of nests around Leuchars air base decreased by 39.17% while the number in all other rookeries increased by 32.17% (X^2 = 101.61, 1 df, $p << 0.001$). The eight (different) rookeries within 2.5 km of Leuchars in 1945 comprised 2,041 nests. This means that

there was, from 1945, a decrease in the number of rooks breeding near Leuchars of 76.48% up to 1975 while the respective decrease for all other rookeries was virtually the same at 76.08%. So clearly, the decrease in rook numbers around Leuchars is a recent phenomenon. It is less clear whether activities at the air base were the cause of the decrease in the late 1970´s. Disturbance of nesting rooks by air traffic could have been responsible if the extent of the disturbance was such to prevent them from carrying out necessary breeding activities. Low flying aircraft, which were frequently present, may have disrupted incubation, but this is unlikely as rooks would be certain to habituate to the noise and sight of them. Similarly, jet fuel exhaust gases, possibly toxic, are not likely to have been a problem as these would be dissipated quickly in the atmosphere. The most likely reasons for the decrease in breeding rook numbers, if R.A.F. exercises were responsible, is desertion of the rookeries by some birds or the failure of these rookeries to attract first time breeders due to excessive noise. However, rookery 42/02, one of the closest to the airfield, increased by 61 nests (to a total of 162) between 1975 and 1977. Although it decreased by 23 nests from 1977 to 1978 its size then was still greater than in 1975. If desertion or failure to adopt the "Leuchars" rookeries was the reason for the decline then why was this rookery an exception? Since 1978 this rookery increased to 180 nests in 1980 but fell to 144 nests in 1983. The "Leuchars" rookeries as a whole showed signs of recovery in the 1980´s (393 nests in 1980, 397 in 1983), but rookery 42/03 became extinct (as it had been in 1977). The causes of the enigmatic decline of these rookeries between 1975 and 1978 remain unknown.

Dutch elm disease and the felling of trees. As far as can be ascertained there have been no effects of Dutch elm disease on

nesting rooks in N.E. Fife. Although in the 1970's there were localised instances of the disease in the area followed by felling and burning of the affected wood none of the trees involved were in rookeries. As pointed out earlier, only just over 1% of rook nests in 1978 were in elm trees, although the figure for 1945 was almost 9%, so elm is not a particularly important tree for nesting rooks in N.E. Fife. Nor was it in Scotland as a whole as only 4.1% of nests were in elm in 1975 (Castle 1977). The distribution of nests over tree genera reported above for N.E. Fife (Table 3.3, p. 86) and for different parts of Britain (Sage & Vernon 1978) illustrate that the rook is fairly catholic in its choice of trees in which to nest (although selectivity of tree species would be difficult to demonstrate - see earlier in this chapter) so disease of any one species is unlikely to affect it adversely unless there are few alternatives to the diseased species. Several other factors mitigate against Dutch elm disease as an important cause of the rook's decline (see previous chapter).

The full extent of the felling of rookeries since the second world war in the study area is not known, nor are the effects on rooks of the felling that has taken place. As explained in chapter 2 redistribution of rooks should be the result of felling, rather than the death or non-breeding of birds. It might be interesting, then, to look at the numbers of breeding rooks in rookeries close to those which were felled. In the mid 1970's to early 1980's four rookeries (31/05, 40/07, 40/08 and 50/01) are known to have been felled.

Rookery 31/05 contained 46 nests in 1975 and was probably felled the following year. Of the three rookeries closest to 31/05 one was not discovered until 1983. Of the other two 31/02 increased between 1975 and 1980 by 32 nests and 30/16 by 4 nests between 1975 and 1978.

Rookery 40/07 contained 20 nests in 1980 and was felled in

1981 or 1982. Of the three rookeries closest to it, two also became extinct in 1980 (40/03 and 40/04) while the other (30/11) increased from 196 nests in 1980 to 463 nests in 1983.

Rookery 40/08 contained 53 nests in 1978 and was probably felled in 1979. The three closest rookeries to 40/08 are 40/09, 40/12 and 40/17. Of these, 40/09 contained 37 nests in 1978 and remained at about this level in 1980 (32 nests) and 1983 (21 nests); 40/12 fell from 186 nests in 1975 to 90 nests in 1978, and rose to 118 nests in 1980 to fall to 79 nests in 1983; and 40/17 held 36 nests in 1978, 41 in 1980 and 38 in 1983.

Rookery 50/01 contained 12 nests in 1975 and was felled in 1976 or 1977. Of the three closest neighbours of 50/01, the largest, 50/02, decreased from 159 nests in 1975 to 99 nests in 1978, and then recovered to 125 nests in 1980 and 113 in 1983; data are not available before 1978 for rookery 51/12; and 50/03 increased by only 1 nest between 1975 and 1978, by a further 2 nests to 1980 and then by a further 61 nests up to 1983.

These figures do not indicate whether redistribution of rooks from felled rookeries took place. They do indicate that minimal changes in the sizes of neighbouring rookeries occurred after felling, suggesting perhaps that little redistribution, at least on a local basis, happened. There was, however, a large increase in rookery 30/11 after felling of 40/07, and so perhaps birds from the latter were absorbed in this growth. New rookeries seem not to have been founded near felled ones in the short time covered by this study, although rookery 42/05 appeared to have been founded in the early 1970's following felling of a rookery close to the present day site.

In addition to the above four rookeries which were completely felled, another two were partially felled during the

period in question. Trees in rookery 41/09 were reduced by less than 25% of their number in the late 1970's but despite this the number of nests in the rookery almost doubled by 1980 and increased again up to 1983. From 1978 onwards rookery 50/05 was subjected to felling on a large scale to make way for holiday chalets. Despite the owner's determination to exterminate the rooks here they have remained, but at a much reduced level (1975 - 195 nests, 1977 - 184, 1978 - 225, and after intensive shooting in 1979, 1980 - 145, 1983 - 60 nests). The three closest rookeries to 50/05 (50/03, 50/04 and 50/07) showed little change between 1978 and 1980, but 50/03 increased from 30 to 91 nests between 1980 and 1983, and 50/07 from 108 to 166 nests in the same period. Perhaps some redistribution of rooks from 50/05 occurred here.

There is little evidence that felling of trees produced any marked change in rook numbers between 1956 and 1978, although large rookeries which existed in 1945 were felled (see earlier). Similarly, there is no good evidence from the few available data to suggest that rooks adopt nearby rookeries when their own rookery is felled.

Pesticides. As with the rook population of Britain, the effects of pesticides on the rook in N.E. Fife are not known for certain. Organo-chlorine compounds, including those of the cyclodiene group, were in use in the study area in the 1950's and 1960's and so might have at least contributed to the population decline. There are virtually no data on rook numbers in N.E. Fife during the 1950's and 1960's and so the exact timing of the decline cannot be related to the peak time of organo-chlorine insecticide use.

Agriculture. Perhaps the most important factor affecting rook numbers is the bird's food supply and therefore the way the land is used by humans. Chapter 2 briefly addressed the ways in which changes in agricultural practices made this century might have affected rook populations. Such changes will now be discussed in more detail as they pertain to N.E. Fife.

One major difference in farming methods which must have affected rooks to some extent is that stooks of grain are no longer left in fields after harvesting. It is not known when this practice ceased in N.E. Fife but it appears to have persisted up to the mid 1950's at least. An R.A.F. Leuchars aerial photograph of the area between St. Andrews and the village of Guardbridge (including the transect area of chapter 4) taken in August 1954, reveals that then there were many stooks in fields. Presumably the present day lack of stooks has resulted in a reduced amount of grain being available to rooks in late summer.

In order to investigate the relationship between rook numbers and land use, the agricultural census data for the N.E. Fife parishes were obtained from the Scottish Records Office in Edinburgh. These contain summaries of such data as the areas of land used for different purposes and are submitted annually by farmers. Using them it is possible to assess the densities of breeding rooks in relation to the areas of land under various farm crops.

Several authors have previously reported such densities, although the method of presenting them has differed. Usually, they are given as acres of land per nest, but here all figures have been converted to hectares per breeding rook. Some densities have been extrapolated from published accounts when these have not been calculated by the authors.

Tucker (1935) reported rook densities for his rookeries

survey of Somerset in 1933-34, and also summarised the findings of other workers up to that time. In several counties from the Isle of Wight to Dumfriess, mostly in the 1920's, the number of hectares of land under crops and grass combined per adult breeding rook ranged from 3.04 in the Upper Thames region and in the Isle of Wight to the much less dense 17.01 in N. Wales. A higher density, 3.00 ha/bird, was found in 1939 in part of Shropshire (Lloyd 1940), while Sage (1972) noted 6.82, 3.46 and 4.99 ha/bird in Hertfordshire in 1945, 1961 and 1971 respectively.

The densities recorded with respect to arable land only in the Midlands between 1928 and 1930 ranged from 1.23 to 8.75 ha/bird (Roebuck 1933). Even higher densities were recorded by Tucker (1935) in Somerset in 1933-34 (0.75 ha/bird) and by Lloyd (1940) in the Shrewsbury area in 1939 (0.73 ha/bird). Between 1928 and 1962 in Nottinghamshire, Dobbs (1964) recorded densities of 2.39 to 6.30 ha/bird. In Hertfordshire, Sage (1972) reported figures of 5.07, 2.54 and 3.99 ha/bird for 1945, 1961 and 1971, while Yapp's (1951) ranged from 1.89 to 11.11 ha/bird between 1933 and 1944 in W. Gloucestershire.

The density of rooks in relation to root crops in Ayrshire was 0.12 ha/bird in both 1956 and 1966 (Castle 1968). In relation to cereals, root crops and potatoes combined in W. Gloucestershire between 1933 and 1944 it ranged from 1.54 to 11.11 ha/bird (Yapp 1951).

The area of land under cereals per breeding rook has also varied much. Highest densities were in Ayrshire in 1956 with 0.28 ha/bird and 1966 with 0.33 ha/bird (Castle 1968). Tucker (1935) reported 0.29 ha/bird in Somerset in 1933. The figures for Nottinghamshire between 1928 and 1962 ranged from 1.69 to 2.87 ha/bird, and in Hertfordshire between 1945 and 1971, from 1.57 to

2.97 ha/bird (Dobbs 1964, Sage 1972). Corresponding figures for W. Gloucestershire between 1933 and 1944 were 1.20 to 8.33 ha/bird (Yapp 1951).

With regard to grassland Roebuck (1933) gave densities of between 2.19 and 8.16 ha/bird in several parts of the Midlands between 1928 and 1930, and in Nottinghamshire, Dobbs (1964) reported figures of 6.75 ha/bird in 1928, 7.47 ha/bird in 1932, 3.68 ha/bird in 1944, 2.32 ha/bird in 1958 and 3.72 ha/bird in 1962. The highest density of breeding rooks in relation to grassland was recorded by Sage (1972) in Hertfordshire. In 1971 this was 1.60 ha/bird, the same density as ten years earlier, but an increase on the density of 2.93 ha/bird in 1945. High densities were also noted by Tucker (1935) in Somerset in 1933-34 (3.75 ha/bird), by Lloyd (1940) in the Shrewsbury area in 1939 (2.27 ha/bird) and by Castle (1968) in Ayrshire (1.82 ha/bird in 1956 and 2.70 ha/bird in 1966).

Although the wide ranges of densities noted above would seem to point to no clear relationship between rook numbers and land use it is perhaps worth stating that the smallest ranges are for grassland and for cereals, two important feeding stations for rooks. There is no obvious temporal pattern to the figures, and therefore no suggestion that variation in rook numbers is linked with the changes in land use which have occurred within geographical regions over the years. This method of examining the possible connections between land use and rook population size is, however, crude, and may disguise real associations.

In N.E. Fife in 1945 and 1978 the following densities (ha/bird) prevailed. (The categories in this table match those used by the authors mentioned above, and were devised partly in order to permit comparison with those data presented for other areas in various years. Some categories appear somewhat arbitrarily defined,

e.g. cereals, root crops and potatoes as contrived by Yapp (1951), but the nature of agricultural statistics summaries is such that the categories used here are certainly the same as those used in the other studies).

	1945	1978
Crops and grass	1.54	5.72
Arable	0.95	3.66
Root crops	0.13	0.19
Cereals, root crops and potatoes	0.85	3.41
Cereals	0.54	2.88
Grass	0.60	2.05

Clearly, the density of rooks in relation to the use of land for all agricultural purposes other than the cultivation of root crops declined markedly between 1945 and 1978. These figures do not suggest which field types are necessary for rook survival. This may be examined by attempting to correlate areas of land put to different uses with rook numbers. Previous authors who have shown a correlation between breeding rook numbers and land use include Castle (in Sage & Vernon 1978) who found a significant positive correlation between rook numbers and area of land under grass, and a significant negative correlation between rook numbers and area of rough grazings in Scotland in 1975. Sage & Vernon (1978) reported that no similar correlations existed in England, but that rook numbers and grassland area were also correlated in Wales. In all of Poland, Dyrcz (1966) failed to find a correlation between rook nests and grassland, but did find a positive correlation between rook nests and area of land used for growing corn (= presumably cereals in general). In one

locality in Poland, however, Luniak (1972) reported that rook numbers were correlated with grassland area but not with the area of land used for growing root crops. Analysis of the figures presented by Dobbs (1964) revealed no significant correlations between rook numbers in Nottinghamshire between 1928 and 1962 and the areas of land used for crops and grass combined ($r = -0.753$, 3 df, $p > 0.1$), crops ($r = 0.213$, 3 df, $p >> 0.1$), grass ($r = -0.703$, 3 df, $p > 0.1$), or cereals ($r = 0.804$, 3 df, $p > 0.1$). Similarly, when Yapp's (1951) data for W. Gloucestershire between 1933 and 1944 were analysed no significant relationship emerged between rook numbers and areas of arable land ($r = 0.547$, 6 df, $p > 0.1$) or cereals ($r = 0.663$, 6 df, $p > 0.1$). As mentioned in chapter 2 an examination of Roebuck's (1933) data for rook populations in the Midlands in years between 1928 and 1930 revealed significant correlations between rook numbers and areas of crops and grass combined and also for arable land. With the effects of total land area partialled out, however, only the correlation between rook numbers and land used for crops and grass remained significant (partial $r = 0.849$, 5 df, $p < 0.02$). In N.E. Fife in 1978 there were significant positive correlations between the number of nests in each parish and the areas of land used for grass, barley, oats, wheat, turnips and swedes, potatoes, rough grazing and woodland. With total land area partialled out, however, there were no significant associations between population size and land put to these uses. In 1945 there were also significant positive correlations between number of nests and all of these with the exception of woodland (data not available) but with the addition of fallow land. Once again, most correlations became non-significant when total land area was partialled out. The exception was a significant positive correlation between number of nests and area of barley (partial $r = 0.498$, 26 df, $p < 0.02$).

Once more, this time having used a correlational approach, the relationships between rook numbers and land use have been shown to be diverse, leading to no unequivocal interpretation of their nature. There are shortcomings with this method. No account is taken of the possibility that land use patterns in years prior to the one in which the size of the rook population is assessed are important. This can be seen to be of possible significance if one considers that the effects of a shortage of food in the breeding season leading to high nestling or juvenile mortality would only be manifest one or two years later when these birds would first have attempted to build a nest and breed. In addition, by using simple bivariate correlations it is not possible to examine the combined effects of variation in areas of land used for each possible purpose, that is no control is exerted over possible intercorrelations between the areas of land put to different uses. In order to overcome these drawbacks an approach using multiple regression was adopted.

To investigate the amount of variation in the population size of N.E. Fife in 1978 due to land use patterns in that year the following data for each parish in the study area were entered into a stepwise multiple regression analysis: number of nests in 1978 (y), total land area (x_1), and the respective areas under grass (x_2), barley (x_3), oats (x_4), wheat (x_5), turnips and swedes (x_6), potatoes (x_7), fallow (x_8), rough grazings (x_9) and woodland (x_{10}). Table 3.7 (pp. 89-92) contains this data.

The equation $y = 33.02 - 0.10x_1 + 0.17x_2 + 0.44x_3 + 0.67x_4 - 0.40x_5 - 2.70x_6 - 0.04x_7 + 4.26x_8 + 0.32x_9 - 0.56x_{10}$ accounts for only 40% of the variation in the population size of each parish in 1978 ($F = 1.08$, 10,16 df, $p > 0.1$). No independent variable accounted for a significant proportion of this variation.

A similar analysis was carried out to discover if land use

in 1977 was a better predictor of rook population size in 1978. This data is shown in Table 3.8 (pp. 93-96). With the labels for each variable identical to those for the 1978 data, the equation $y = 41.68 + 0.06x_1 + 0.24x_2 - 0.27x_3 - 0.48x_4 + 1.10x_5 - 0.32x_6 + 0.77x_7 - 13.67x_8 - 0.43x_9 - 0.72x_{10}$ accounts for 44% of the variation in 1978 population size ($F = 1.25$, 10,16 df, $p > 0.1$). Although more variation is explained here by using land use data for 1977 there were still no independent variables which accounted for a significant amount of this variation.

A third analysis was carried out using land use data for 1976, which are shown in Table 3.9 (pp. 97-100). Again the labels for each variable are as before, but this time 28 as opposed to 27 parishes were included in the analysis. This is because the census returns for Pittenweem were combined with those for Elie & St. Monance by the Department of Agriculture and Fisheries for Scotland in 1977. Using 1976 agricultural data, then, the equation $y = 28.06 - 0.04x_1 + 0.14x_2 + 0.02x_3 - 0.28x_4 + 0.94x_5 + 0.94x_6 - 0.14x_7 - 4.84x_8 + 0.02x_9 - 0.06x_{10}$ accounts for 45% of the variation in population size ($F = 1.39$, 10,17 df, $p > 0.1$). Once again, although more variation in 1978 population size is explained by the 1976 than either the 1977 or 1978 land use data, no variables accounted for a statistically significant amount of this variation. It does seem, however, that land use in a particular year may only be notable in its full effects on the rook population two years later. Some effect is apparent even one year later.

Identical analyses were performed in examination of the 1945 population of rooks in the study area. For agricultural census purposes the amalgamation took place in 1973 of the parish of Newburgh with Scoonie, and of Cupar with Cults. The data from each of these pairs, however, was combined in the following analyses, so

that data from 28 parishes were considered. Labels for variables are the same as the 1970's analyses but areas of woodland (x_{10}) were not available in the 1940's.

Table 3.10 (pp. 101-104) shows the land use data and rook population size for each parish in the study area in 1945. The equation $y = 84.04 - 0.03x_1 + 0.30x_2 + 5.43x_3 - 0.24x_4 + 1.48x_5 - 3.55x_6 - 2.33x_7 + 6.58x_8 + 1.19x_9$ significantly accounts for 65% of the variation in 1945 population size ($F = 3.72$, 9,18 df, $p < 0.01$). Despite this, no independent variable contributed significantly in explaining the variation, although area of land under barley (x_3) came close ($t = 1.98$, 18 df, $0.1 > p > 0.05$), accounting for 53% of the variation in the dependent variable.

Using agricultural data for 1944, the equation $y = -29.94 + 0.04x_1 + 1.01x_2 + 1.84x_3 - 2.81x_4 + 3.25x_5 - 1.68x_6 - 1.04x_7 - 1.92x_8 + 1.85x_9$ significantly accounts for 69% of the variation in 1945 population size ($F = 4.41$, 9,18 df, $p < 0.01$). Again only one variable came close to explaining a significant proportion of this. This was area of land under rough grazings (x_9) which accounts for 18% of the variation ($t = 2.04$, 18 df, $0.1 > p > 0.05$). The data used in this analysis is contained in Table 3.11 (pp. 105-108).

Table 3.12 (pp. 109-112) contains 1943 agricultural data. The multiple regression equation $y = 16.64 + 0.02x_1 + 1.39x_2 + 0.01x_3 - 2.47x_4 + 3.44x_5 - 1.03x_6 - 1.40x_7 - 18.28x_8 + 0.95x_9$ significantly explains 75% of the variation in 1945 population size ($F = 5.85$, 9,18 df, $p < 0.01$). Two variables significantly contribute to this figure. The first, area of land under wheat (x_5), accounts for 58% of the variation ($t = 2.64$, 18 df, $p < 0.05$). The second, area of grassland (x_2), accounts for a further 1% ($t = 2.29$, 18 df, $p < 0.05$).

As with the 1970's data, then, the size of the rook

population in 1945 was best predicted by the agricultural profile of the land two years earlier. Also, the 1944 agricultural data were better predictors of 1945 population size than the 1945 data. It would appear that if the nature of rook feeding grounds is important in governing the numbers of birds that survive to breed then there is a time lag before this is manifested. The relationships between rook numbers and areas of wheat and grass are interesting. Parishes with large areas of each in 1943 tended to have more birds breeding (or at least building a nest) in them in 1945, and those with small areas of each had fewer numbers of breeding birds. This suggests that the quantity of food available from these field types may have been an important determinant of rook survival. If so, the crucial time of year is likely to have been late spring to winter 1943/44. During the present study in N.E. Fife grassland was the most heavily used foraging station of rooks during and after the nestling period in late spring to summer and also in the winter. Cereal stubble was the most important field type in between these times and was also very important in winter (see chapter 4). Presumably this was also the case in the 1940's given that the temporal pattern of crop growth has not changed much since then. In fact, in the 1940's wheat stubble fields may have been relatively more important as feeding sites than were barley stubble fields in the 1970's because 1) a greater quantity of spilled grain would be available due to relatively inefficient harvesting methods and also due to the practice of building stooks and 2) wheat is a preferred component of the grain diet of rooks (Luniak 1977).

The evidence presented here, while circumstantial, points to the survival rate of rooks due to food availability in their first year of life in 1943/44 as a significant determinant of population size in 1945. The two year time lag suggests that it was the

survival of young rooks hatched in 1943 which was crucial, these birds being most sensitive to variations in food availability. Given the importance of area of land under wheat as a predictor variable then the fact that this stood at 6,005 ha in 1943 and at almost half this level, 3,152 ha, in 1945 may mean that the 1945 population size was greater than the 1947 size. Any decrease in rook numbers between 1945 and 1947, however, could have been slightly offset by the increase in the area of grassland during this time of almost 3,000 ha. Since the area of grassland in the study area in 1978 was 17,274 ha compared with 17,920 ha in 1945, while the area under wheat fell to 1,770 ha in 1978 from 3,152 ha in 1945, the large decrease in the size of the rook population during these 33 years may have been due to the reduced area of land used for wheat. The time when a shortage of cereal diet would probably have occurred is winter, when stubble fields would most likely to have been depleted of spilled wheat grains. This would have resulted from heavy utilisation of these fields during late summer/autumn. The consequence of this should have been greater mortality of young rooks in the winter. This is supported to a large degree by published data on rook mortality. Holyoak (1971) showed that the heaviest mortality among rooks in their first year of life occurred in the winter (that is in the winter of their second calendar year of life).

If aspects of land use were important in governing rook numbers in the 1940's why was there no similar association in the 1970's? If the size of the rook population declined gradually from the 1940's as wheat areas did and as certain types of grassland did, then one would perhaps expect there still to have been an observable relationship between these in the 1970's. The finding that no land use data significantly accounts for variations in population size in the 1970's suggests that there came a point between the 1940's and

1970's when the dependence of rook numbers on areas of land under wheat and grass was broken. Whether this happened because of the reduction in wheat cultivation and areas of old grassland or for some other reason is unknown. Conceivably, either or both could have resulted in a population crash. A steady decline in important field types would not necessarily be mirrored in a steady decline in rook numbers if there was intense competition between birds resulting from reduced food availability. Disproportionately high mortality could have been the outcome of this despite 1) the adaptation of asynchronous hatching of eggs to alleviate the effects of food shortage in the breeding season (Lockie 1955), and 2) the consequences of a possible hierarchy (not necessarily a stable one) at localised food sources in winter (Feare et al 1974, Patterson 1975). Equally, some other factor could have been responsible for the severance of the association between rook numbers and land use patterns, such as heavy mortality caused by pesticide use. If other factors were responsible, and these are no longer prevalent, then the recovery of the population which seems to be taking place might be being hindered because of changes in land use. Rook numbers may not yet have reached a level which reflects the altered relative proportions of land used for different cereals and for other purposes.

The precise reasons for the decline and subsequent geographical dispersion and structure of the N.E. Fife rook population remain problematic. Although some important reasons have been highlighted here the crucial data (i.e. population counts for years between 1945 and 1975) do not exist. While pesticides may have been a cause of decline in this part of Scotland and other factors were probably not responsible, it is likely that the renewed economic importance of agriculture in Britain since the second world war had a

major impact on this, and other, rook populations. There can be little doubt that improved harvesting methods and a swing to barley as the main cereal crop has led to not only a reduction in the quantity of exploitable grain available to rooks but also a reduction in the overall quality. Barley grains require more handling time for de-husking before they are ingested than do oats, and of course wheat requires no de-husking. The nature of the association between rook populations and agricultural practices is likely to be further complicated in the future as advances are made in the development and cultivation of autumn sown cereals. Land use by rooks in N.E. Fife in the 1970's is explored fully in the next two chapters.

Table 3.1. Distribution by size of rookeries found in 1978.

No. of nests	No. of rookeries	% of total
1-25	28	38.89
26-50	15	20.83
51-100	14	19.44
101-200	12	16.67
201-300	2	2.78
301-400	1	1.39

Table 3.2. Number of nests in each rookery size group in 1978.

Size of rookery (in nos. of nests)	No. of nests counted	% of total no. nests
1-25	232	5.50
26-50	494	11.71
51-100	1025	24.29
101-200	1630	38.63
201-300	497	11.78
301-400	342	8.10
Total	4220	100

Table 3.3. The numbers of nests contained in the various tree genera in 1978. English names of trees are: Fagus - beech; Acer - sycamore; Ulmus - elm; Quercus - oak; Fraxinus - ash; Aesculus - horse chestnut; Pinus - pine; Picea - spruce; Larix - larch; Araucaria - Chile pine; Cupressus - cypress.

Tree genus	No. of nests	% of total
Pinus	1965	46.56
Fagus	1132	26.82
Acer	553	13.10
Quercus	209	4.95
Ulmus	202	4.79
Picea	45	1.07
Larix	41	0.97
Fraxinus	39	0.92
Aesculus	14	0.33
Araucaria	9	0.21
Cupressus	4	0.09
Unidentified (Broadleaved)	7	0.17
Coniferous	2064	48.91
Broadleaved	2156	51.09

Table 3.4. The distribution of rookeries by altitude in 1978. Rookeries which were not counted in the 1978 survey have been included.

Altitude (ft.)	No. of rookeries (% of total)	Av. rookery size (nests)
<100	24 (30.77)	30.80
100-199	11 (14.10)	57.36
200-299	9 (11.54)	94.83
300-399	11 (14.10)	81.73
400-499	6 (7.69)	45.60
500-599	11 (14.10)	75.40
600-699	6 (7.69)	55.50

Table 3.5. The numbers of rookeries on various geological substrata in 1978. Rookeries which were not counted in the 1978 survey have been included.

Geological substratum	No. of rookeries (% of total)	Av. rookery size (nests)
Andesitic lavas	7 (8.97)	116.71
Calciferous sandstone	31 (39.74)	72.62
Carboniferous limestone	10 (12.82)	39.00
Coal measures	5 (6.41)	6.00
Dolerite	13 (16.67)	51.08
Marine alluvium	4 (5.13)	31.50
Millstone grit	1 (1.28)	122.00
Old red sandstone	7 (8.97)	33.43

Table 3.6. The number of nests in selected rookeries in 1978 (y) in relation to their altitude in feet above sea level (x_1), the number of nests they contained in 1945 (x_2) and the distance in km to the nearest rookery in 1975 (x_3).

Rookery	y	x_1	x_2	x_3
30/03	0	575	30	0.20
30/04	21	425	75	0.25
30/12	2	125	691	0.38
30/16	154	250	97	4.47
31/01	68	300	245	1.92
31/06	28	100	194	0.51
31/07	9	75	32	0.40
32/03	25	300	549	0.94
40/01	31	50	10	2.90
40/05	7	125	131	4.11
40/06	1	150	3	4.11
40/07	20	50	95	0.50
40/10	12	625	757	0.16
41/03	272	350	559	3.66
41/05	30	75	446	1.55
41/14	31	50	227	0.15
42/04	61	25	528	0.88
42/05	11	75	101	1.36
50/03	28	300	93	1.53
50/04	112	200	312	2.01
50/05	225	100	325	2.15
51/03	5	25	145	0.47
51/05	11	100	19	0.23
60/01	154	150	764	1.48
60/03	9	100	123	1.48

Table 3.7. The number of nests in N.E. Fife parishes in 1978 (y) in relation to the total land area of each parish (x_1) and the areas in 1978 of grass (x_2), barley (x_3), oats (x_4), wheat (x_5), turnips and swedes (x_6), potatoes (x_7), fallow land (x_8), rough grazings (x_9) and woodland (x_{10}). All areas are in hectares.

Parish	y	x_1	x_2	x_3	x_4
Anstruther & Carnbee	365	4100.61	1558.70	1676.10	60.80
Balmerino	0	1120.45	169.10	529.00	44.10
Cameron	302	2946.26	1163.80	940.20	108.90
Ceres	287	3737.86	1700.90	1224.40	86.70
Crail	262	2111.74	632.80	990.30	48.20
Creich	52	1069.33	313.60	455.50	0.00
Cults & Cupar	111	2377.73	836.80	962.30	35.40
Dairsie	272	985.73	242.30	526.30	17.20
Elie & St. Monance	141	822.98	194.10	360.90	3.60
Dunino	102	1391.80	375.50	607.20	48.30
Ferry-Port on Craig	0	580.06	243.80	206.90	8.10
Flisk	16	879.55	248.10	412.30	4.00
Forgan	105	1548.08	477.40	655.80	13.50
Kemback	0	826.11	261.40	325.20	50.30
Kennoway	170	994.03	239.00	444.10	4.80
Kettle	154	2782.29	821.20	1244.40	8.50
Kilconquhar	85	2512.45	1206.00	1106.80	56.80
Kilmany	30	1813.77	588.20	702.50	40.00
Kilrenny	0	1305.77	311.50	637.50	26.60
Kingsbarns	477	1463.87	419.80	717.30	12.00
Largo	290	2383.81	916.30	866.10	56.20
Leuchars	262	3588.87	806.40	1449.10	114.00
Logie	0	961.44	464.40	397.70	36.00

Table 3.7 (continued)

Parish	y	x_1	x_2	x_3	x_4
Monimail & Moonzie	342	3129.15	959.90	1194.50	157.40
Newburgh & Scoonie	218	1473.38	585.40	607.90	30.70
Newburn	8	1091.70	273.10	304.70	15.30
St. Andrews & St. Leonards	169	4116.40	1264.10	1807.10	116.70

Table 3.7 (continued)

Parish	x_5	x_6	x_7	x_8	x_9	x_{10}
Anstruther & Carnbee	171.20	101.70	171.30	0.40	156.60	52.60
Balmerino	128.20	34.00	81.40	0.00	59.80	8.50
Cameron	162.50	45.70	64.00	21.20	151.70	123.30
Ceres	31.40	98.10	160.10	0.00	124.40	91.60
Crail	78.60	77.80	105.10	0.00	36.60	18.70
Creich	30.50	11.30	62.90	1.20	73.00	8.10
Cults & Cupar	33.50	102.40	126.30	5.50	124.10	29.10
Dairsie	15.30	8.40	32.40	0.00	21.40	8.00
Elie & St. Monance	31.60	37.50	81.60	0.00	26.50	0.00
Dunino	60.30	42.70	111.40	0.00	25.80	66.20
Ferry-Port on Craig	24.80	18.30	28.20	5.20	4.50	8.40
Flisk	16.40	25.50	49.00	0.00	52.20	0.00
Forgan	39.10	61.90	54.10	0.40	38.70	10.00
Kemback	16.10	18.40	28.90	0.00	4.40	45.80
Kennoway	19.80	24.40	67.50	0.60	10.80	9.00
Kettle	46.70	78.50	184.20	2.00	118.80	40.20
Kilconquhar	19.50	108.20	156.00	0.30	92.60	58.50
Kilmany	44.70	64.50	104.20	0.00	107.70	17.40
Kilrenny	79.60	45.50	95.30	0.60	20.80	1.60
Kingsbarns	55.90	46.50	105.30	0.00	41.70	10.30
Largo	163.50	54.80	119.70	19.70	74.40	42.10
Leuchars	204.80	98.30	171.00	7.00	482.70	76.30
Logie	61.60	44.90	43.10	1.50	51.80	34.80

Table 3.7 (continued)

Parish	x_5	x_6	x_7	x_8	x_9	x_{10}
Monimail & Moonzie	13.90	134.90	235.30	0.30	265.20	14.20
Newburgh & Scoonie	97.10	45.50	89.30	0.00	194.50	92.80
Newburn	15.60	19.60	22.20	0.00	14.30	6.50
St. Andrews & St. Leonards	107.90	143.30	318.70	0.00	129.20	25.80

Table 3.8. The number of nests in N.E. Fife parishes in 1978 (y) in relation to the total land area of each parish (x_1) and the areas in 1977 of grass (x_2), barley (x_3), oats (x_4), wheat (x_5), turnips and swedes (x_6), potatoes (x_7), fallow land (x_8), rough grazings (x_9) and woodland (x_{10}). All areas are in hectares.

Parish	y	x_1	x_2	x_3	x_4
Anstruther & Carnbee	365	4100.61	1564.30	1500.40	80.50
Balmerino	0	1120.45	173.00	497.90	51.80
Cameron	302	2946.26	1246.60	882.30	100.80
Ceres	287	3737.86	1764.30	1128.80	91.80
Crail	262	2111.74	726.50	861.10	53.30
Creich	52	1069.33	296.80	426.40	0.00
Cults & Cupar	111	2377.73	847.20	926.60	45.20
Dairsie	272	985.73	299.60	421.12	8.00
Elie & St. Monance	141	822.98	160.80	385.90	2.40
Dunino	102	1391.80	350.10	557.70	47.50
Ferry-Port on Craig	0	580.06	215.30	213.70	18.20
Flisk	16	879.55	256.70	374.40	1.60
Forgan	105	1548.08	505.90	632.90	8.10
Kemback	0	826.11	259.80	352.10	41.80
Kennoway	170	994.03	239.40	439.70	6.00
Kettle	154	2782.29	850.00	1199.20	17.80
Kilconquhar	85	2512.45	1139.80	1014.00	81.80
Kilmany	30	1813.77	561.10	707.70	76.40
Kilrenny	0	1305.77	337.80	585.60	31.10
Kingsbarns	477	1463.87	401.70	717.90	22.90
Largo	290	2383.81	947.40	812.10	96.80
Leuchars	262	3588.87	1310.20	1459.40	90.00
Logie	0	961.44	382.90	393.40	33.00

Table 3.8 (continued)

Parish	y	x_1	x_2	x_3	x_4
Monimail & Moonzie	342	3129.15	941.70	1136.10	155.10
Newburgh & Scoonie	218	1473.38	630.50	585.40	38.30
Newburn	8	1091.70	247.30	296.80	17.40
St. Andrews St. Leonards	169	4116.40	1229.20	1858.20	107.30

Table 3.8 (continued)

Parish	x_5	x_6	x_7	x_8	x_9	x_{10}
Anstruther & Carnbee	167.60	119.20	190.00	0.00	269.50	48.80
Balmerino	140.10	40.70	82.30	0.00	47.20	11.30
Cameron	186.40	40.60	77.50	8.40	137.10	121.50
Ceres	51.00	97.50	166.90	3.00	122.30	105.10
Crail	67.70	100.40	118.10	0.00	50.70	18.80
Creich	45.90	7.80	90.50	0.30	73.70	8.00
Cults & Cupar	40.50	118.20	137.60	6.50	100.80	40.50
Dairsie	30.50	18.10	51.00	0.20	21.40	13.70
Elie & St. Monance	34.90	34.70	88.50	0.10	31.30	0.00
Dunino	63.60	63.50	143.40	0.00	30.60	78.50
Ferry-Port on Craig	17.00	22.40	39.90	4.10	6.10	9.20
Flisk	24.30	26.50	62.20	0.00	56.20	0.00
Forgan	40.90	74.80	66.20	0.90	85.20	10.00
Kemback	12.00	18.10	34.80	0.00	22.70	37.80
Kennoway	17.10	31.30	76.50	1.20	16.50	2.00
Kettle	47.80	87.70	207.60	3.50	117.30	39.00
Kilconquhar	31.70	127.40	182.50	3.50	114.80	46.30
Kilmany	26.30	74.10	94.40	0.00	107.90	17.80
Kilrenny	55.30	71.20	118.90	0.80	23.00	0.00
Kingsbarns	56.80	54.20	124.40	0.00	15.20	11.80
Largo	142.40	62.20	124.40	7.40	90.50	28.30
Leuchars	137.20	96.90	222.20	5.80	76.60	55.10
Logie	35.90	48.00	34.50	1.00	150.30	32.50

Table 3.8 (continued)

Parish	x_5	x_6	x_7	x_8	x_9	x_{10}
Monimail & Moonzie	86.80	154.20	267.80	0.70	246.50	17.80
Newburgh & Scoonie	82.90	59.40	89.90	0.00	95.60	44.20
Newburn	22.50	19.90	24.00	3.10	18.50	4.00
St. Andrews St. Leonards	118.90	151.00	321.70	3.60	118.80	23.50

Table 3.9. The number of nests in N.E. Fife parishes in 1978 (y) in relation to the total land area of each parish (x_1) and the areas in 1976 of grass (x_2), barley (x_3), oats (x_4), wheat (x_5), turnips and swedes (x_6), potatoes (x_7), fallow land (x_8), rough grazings (x_9) and woodland (x_{10}). All areas are in hectares.

Parish	y	x_1	x_2	x_3	x_4
Anstruther & Carnbee	365	4100.61	1589.20	1566.60	91.80
Balmerino	0	1120.45	158.10	354.30	0.00
Cameron	302	2946.26	1270.40	837.70	109.00
Ceres	287	3737.86	1934.50	1070.50	81.30
Crail	262	2111.74	664.00	890.60	74.90
Creich	52	1069.33	229.80	548.10	0.00
Cults & Cupar	111	2377.73	897.00	921.10	40.30
Dairsie	272	985.73	333.70	373.10	21.40
Elie & St. Monance	141	750.00	191.40	301.10	13.80
Dunino	102	1391.80	383.10	527.30	50.50
Ferry-Port on Craig	0	580.06	229.60	222.00	10.50
Flisk	16	879.55	271.10	395.10	0.00
Forgan	105	1548.08	536.30	660.10	5.20
Kemback	0	826.11	314.50	331.40	35.20
Kennoway	170	994.03	288.10	441.30	7.80
Kettle	154	2782.29	887.00	1093.40	18.00
Kilconquhar	85	2512.45	952.60	951.00	104.60
Kilmany	30	1813.77	582.80	754.00	62.00
Kilrenny	0	1305.77	352.40	557.50	35.20
Kingsbarns	477	1463.87	418.00	672.10	25.70
Largo	290	2383.81	960.50	715.50	105.40
Leuchars	262	3588.87	909.90	1292.00	108.80
Logie	0	961.44	378.10	358.80	42.00

Table 3.9 (continued)

Parish	y	x_1	x_2	x_3	x_4
Monimail & Moonzie	342	3129.15	1045.90	1114.40	166.60
Newburgh & Scoonie	218	1473.38	541.80	502.30	33.30
Newburn	8	1091.70	351.70	438.80	20.00
Pittenweem	0	72.98	2.90	47.80	0.00
St. Andrews & St. Leonards	169	4116.40	1430.10	1553.60	168.00

Table 3.9 (continued)

Parish	x_5	x_6	x_7	x_8	x_9	x_{10}
Anstruther & Carnbee	213.90	128.70	163.20	1.90	154.40	46.20
Balmerino	28.20	35.10	47.40	0.00	37.10	2.00
Cameron	225.40	59.60	42.60	0.00	143.80	124.10
Ceres	62.70	101.30	150.30	7.40	85.60	99.90
Crail	81.40	106.80	80.30	0.00	48.90	15.80
Creich	34.60	4.00	93.80	0.20	99.30	40.90
Cults & Cupar	33.10	95.70	123.80	2.70	101.50	34.50
Dairsie	52.80	18.50	77.30	0.00	21.40	13.20
Elie & St. Monance	58.50	30.70	88.30	0.00	8.10	0.00
Dunino	93.70	64.00	136.80	0.00	26.70	64.20
Ferry-Port on Craig	18.80	25.80	38.10	3.00	7.50	9.20
Flisk	13.70	21.40	46.10	0.00	52.30	1.20
Forgan	40.50	50.90	61.80	0.80	90.30	10.00
Kemback	18.50	35.60	35.00	0.00	6.40	36.90
Kennoway	35.30	33.90	80.50	2.60	16.00	8.40
Kettle	103.00	77.90	227.20	3.20	118.90	39.30
Kilconquhar	34.70	100.10	184.20	0.00	51.50	32.40
Kilmany	51.40	63.10	111.20	13.70	147.20	17.70
Kilrenny	65.60	66.60	111.80	0.40	60.80	0.10
Kingsbarns	101.60	59.30	106.60	0.40	13.70	24.40
Largo	218.20	57.10	118.70	9.20	81.30	36.00
Leuchars	159.40	151.10	208.60	4.70	507.20	74.10
Logie	62.60	56.20	46.30	2.00	157.30	31.50

Table 3.9 (continued)

Parish	x_5	x_6	x_7	x_8	x_9	x_{10}
Monimail & Moonzie	19.70	164.30	214.20	0.70	274.90	21.70
Newburgh & Scoonie	74.40	42.80	78.00	0.00	78.90	45.40
Newburn	19.70	26.80	28.40	0.80	71.70	26.20
Pittenweem	0.00	0.00	9.60	0.00	10.30	0.00
St. Andrews & St. Leonards	183.80	164.40	318.30	0.40	94.00	26.70

Table 3.10. The number of nests in N.E. Fife parishes in 1945 (y) in relation to the total land area of each parish (x_1) and the areas in 1945 of grass (x_2), barley (x_3), oats (x_4), wheat (x_5), turnips and swedes (x_6), potatoes (x_7), fallow land (x_8) and rough grazings (x_9). All areas are in hectares.

Parish	y	x_1	x_2	x_3	x_4
Anstruther & Carnbee	889	4100.61	1564.47	306.28	485.83
Balmerino	0	1120.45	317.31	122.17	182.89
Cameron	1305	2946.26	1335.02	241.60	435.12
Ceres	642	3737.86	1441.80	399.39	616.09
Crail	887	2111.74	589.27	264.47	453.95
Creich	0	1069.33	261.74	63.97	129.96
Cults & Cupar	941	2377.73	1019.95	224.40	447.68
Dairsie	572	985.73	343.22	104.25	132.49
Elie & St. Monance	41	750.00	143.93	65.99	64.88
Dunino	241	1391.80	593.52	81.17	194.74
Ferry-Port on Craig	144	580.06	137.04	39.47	67.00
Flisk	103	879.55	291.60	64.78	124.09
Forgan	265	1548.08	512.85	130.87	244.53
Kemback	403	826.11	323.28	80.36	130.06
Kennoway	85	994.03	402.02	101.62	298.89
Kettle	134	2782.29	819.23	233.10	528.24
Kilconquhar	1	2512.45	1036.74	196.56	385.12
Kilmany	587	1813.77	727.13	179.96	308.91
Kilrenny	646	1305.77	453.24	202.33	278.04
Kingsbarns	699	1463.87	453.24	177.43	260.93
Largo	1357	2383.81	922.47	244.03	399.09
Leuchars	1595	3588.87	993.02	356.88	490.38
Logie	0	961.44	390.79	140.18	190.89

Table 3.10 (continued)

Parish	y	x_1	x_2	x_3	x_4
Monimail & Moonzie	277	3129.15	179.45	45.75	74.90
Newburgh & Scoonie	880	1473.38	753.24	207.18	331.17
Newburn	134	1091.70	379.96	106.48	188.46
Pittenweem	356	72.98	40.38	37.65	18.02
St. Andrews & St. Leonards	1282	4116.40	1494.03	478.04	656.07

Table 3.10 (continued)

Parish	x_5	x_6	x_7	x_8	x_9
Anstruther & Carnbee	190.89	202.83	245.04	10.93	79.96
Balmerino	114.27	139.47	162.96	0.00	49.19
Cameron	62.65	172.57	230.87	17.11	234.31
Ceres	159.82	280.57	387.35	11.94	210.63
Crail	152.33	148.58	210.93	20.34	26.52
Creich	51.01	68.12	92.71	9.72	131.78
Cults & Cupar	182.49	177.73	284.82	2.83	73.07
Dairsie	110.02	81.58	90.59	14.17	0.00
Elie & St. Monance	59.92	53.44	84.41	0.00	4.45
Dunino	57.09	83.60	107.49	12.55	25.30
Ferry-Port on Craig	48.89	39.37	49.29	0.00	62.35
Flisk	88.46	66.40	129.96	0.00	56.68
Forgan	135.63	132.89	169.43	1.62	230.77
Kemback	53.85	63.66	103.04	12.75	0.20
Kennoway	118.52	113.87	189.58	0.00	36.03
Kettle	108.70	218.52	322.98	0.40	238.16
Kilconquhar	109.51	148.38	302.94	25.91	59.11
Kilmany	141.60	165.69	215.28	0.20	14.57
Kilrenny	89.27	124.60	161.44	9.11	17.00
Kingsbarns	113.56	108.70	160.22	14.37	0.00
Largo	91.70	157.39	217.41	14.78	166.60
Leuchars	257.49	239.37	413.36	13.56	440.89
Logie	102.63	104.35	140.28	0.00	145.65

Table 3.10 (continued)

Parish	x_5	x_6	x_7	x_8	x_9
Monimail & Moonzie	62.65	42.51	58.10	0.00	0.00
Newburgh & Scoonie	99.60	194.63	250.71	6.07	161.64
Newburn	41.90	69.03	97.98	0.40	152.22
Pittenweem	4.45	8.30	23.99	0.00	0.81
St. Andrews & St. Leonards	343.52	334.01	440.79	24.09	91.09

Table 3.11. The number of nests in N.E. Fife parishes in 1945 (y) in relation to the total land area of each parish (x_1) and the areas in 1944 of grass (x_2), barley (x_3), oats (x_4), wheat (x_5), turnips and swedes (x_6), potatoes (x_7), fallow land (x_8) and rough grazings (x_9). All areas are in hectares.

Parish	y	x_1	x_2	x_3	x_4
Anstruther & Carnbee	889	4100.61	1238.66	305.97	528.64
Balmerino	0	1120.45	303.04	121.86	185.63
Cameron	1305	2946.26	1187.75	252.02	396.76
Ceres	642	3737.86	1190.08	352.73	603.34
Crail	887	2111.74	519.53	222.06	363.36
Creich	0	1069.33	231.58	72.06	126.82
Cults & Cupar	941	2377.73	920.44	224.29	332.49
Dairsie	572	985.73	310.12	97.87	106.98
Elie & St. Monance	41	750.00	143.82	59.92	59.51
Dunino	241	1391.80	459.92	101.62	214.98
Ferry-Port on Craig	144	580.06	121.66	49.19	60.73
Flisk	103	879.55	245.65	64.37	100.71
Forgan	265	1548.08	463.36	117.21	236.64
Kemback	403	826.11	300.00	81.68	106.38
Kennoway	85	994.03	376.62	100.10	232.49
Kettle	134	2782.29	747.07	196.86	510.63
Kilconquhar	1	2512.45	849.50	183.10	380.77
Kilmany	587	1813.77	653.45	197.67	300.10
Kilrenny	646	1305.77	425.30	162.96	223.79
Kingsbarns	699	1463.87	389.88	179.76	205.87
Largo	1357	2383.81	778.64	199.39	383.91
Leuchars	1595	3588.87	886.94	289.17	491.09
Logie	0	961.44	338.56	122.98	191.60

Table 3.11 (continued)

Parish	y	x_1	x_2	x_3	x_4
Monimail & Moonzie	277	3129.15	154.46	48.18	75.71
Newburgh & Scoonie	880	1473.38	681.57	157.39	290.49
Newburn	134	1091.70	354.65	86.23	143.52
Pittenweem	356	72.98	35.53	30.97	13.77
St. Andrews & St. Leonards	1282	4116.40	1332.69	465.28	576.11

Table 3.11 (continued)

Parish	x_5	x_6	x_7	x_8	x_9
Anstruther & Carnbee	353.64	199.90	271.05	24.29	79.96
Balmerino	121.05	122.47	165.49	0.00	49.19
Cameron	191.80	210.22	231.98	8.30	231.88
Ceres	316.60	257.49	382.19	0.00	253.14
Crail	345.95	136.84	39.17	2.43	22.47
Creich	85.53	67.71	91.30	1.21	121.96
Cults & Cupar	284.32	166.90	305.67	7.89	143.32
Dairsie	143.42	79.35	99.70	8.70	0.00
Elie & St. Monance	71.86	55.47	83.81	1.62	4.45
Dunino	115.38	79.45	124.09	5.67	26.62
Ferry-Port on Craig	44.03	35.02	48.38	4.86	62.35
Flisk	108.00	74.09	151.82	0.00	68.42
Forgan	176.92	138.98	196.15	0.00	230.77
Kemback	110.12	62.45	104.86	0.00	0.20
Kennoway	191.90	110.12	193.93	1.82	35.22
Kettle	178.95	231.68	345.44	0.10	243.62
Kilconquhar	166.09	152.63	329.35	11.74	60.93
Kilmany	174.80	102.94	231.78	0.00	12.55
Kilrenny	186.64	121.05	168.22	2.43	17.00
Kingsbarns	226.92	109.51	154.45	2.02	0.00
Largo	229.86	168.72	251.42	8.91	166.60
Leuchars	349.90	233.40	420.55	14.17	432.19
Logie	128.85	115.38	151.52	0.40	151.72

Table 3.11 (continued)

Parish	x_5	x_6	x_7	x_8	x_9
Monimail & Moonzie	60.53	53.44	59.11	0.00	0.00
Newburgh & Scoonie	209.32	186.13	299.39	0.81	157.18
Newburn	85.22	76.72	121.46	0.00	152.23
Pittenweem	4.86	18.83	28.14	0.00	0.81
St. Andrews & St. Leonards	507.79	331.78	470.45	34.31	91.09

Table 3.12. The number of nests in N.E. Fife parishes in 1945 (y) in relation to the total land area of each parish (x_1) and the areas in 1943 of grass (x_2), barley (x_3), oats (x_4), wheat (x_5), turnips and swedes (x_6), potatoes (x_7), fallow land (x_8) and rough grazings (x_9). All areas are in hectares.

Parish	y	x_1	x_2	x_3	x_4
Anstruther & Carnbee	889	4100.61	1152.54	308.91	562.15
Balmerino	0	1120.45	284.82	93.62	231.07
Cameron	1305	2946.26	1120.25	213.56	461.44
Ceres	642	3737.86	1198.79	322.06	588.87
Crail	887	2111.74	518.63	208.20	379.15
Creich	0	1069.33	248.38	59.51	123.58
Cults & Cupar	941	2377.73	909.71	191.70	379.45
Dairsie	572	985.73	318.32	87.55	115.99
Elie & St. Monance	41	750.00	143.32	55.47	67.41
Dunino	241	1391.80	517.62	86.03	187.04
Ferry-Port on Craig	144	580.06	108.71	40.28	85.02
Flisk	103	879.55	234.11	78.34	135.43
Forgan	265	1548.08	443.12	87.45	275.51
Kemback	403	826.11	289.58	72.17	101.32
Kennoway	85	994.03	372.26	86.84	261.23
Kettle	134	2782.29	730.26	174.70	477.02
Kilconquhar	1	2512.45	794.94	203.64	348.68
Kilmany	587	1813.77	587.35	205.16	308.70
Kilrenny	646	1305.77	433.60	195.24	208.10
Kingsbarns	699	1463.87	398.98	190.28	203.64
Largo	1357	2383.81	800.50	248.38	331.38
Leuchars	1595	3588.87	923.39	279.76	471.86
Logie	0	961.44	349.70	123.79	179.55

Table 3.12 (continued)

Parish	y	x_1	x_2	x_3	x_4
Monimail & Moonzie	277	3129.15	146.36	41.70	93.32
Newburgh & Scoonie	880	1473.38	686.04	155.16	321.06
Newburn	134	1091.70	327.03	89.07	171.76
Pittenweem	356	72.98	34.01	28.74	18.72
St. Andrews & St. Leonards	1282	4116.40	1254.36	500.20	602.23

Table 3.12 (continued)

Parish	x_5	x_6	x_7	x_8	x_9
Anstruther & Carnbee	418.42	191.09	262.25	18.32	81.17
Balmerino	138.97	128.64	152.63	0.00	49.09
Cameron	260.32	168.86	196.05	6.48	226.92
Ceres	365.49	250.30	387.15	6.48	260.43
Crail	386.64	136.74	196.86	9.31	26.52
Creich	74.90	67.71	83.91	0.00	121.96
Cults & Cupar	319.53	146.56	297.37	1.01	143.32
Dairsie	179.76	72.87	99.60	0.40	0.00
Elie & St. Monance	79.76	59.51	86.54	0.00	4.45
Dunino	136.03	65.79	123.68	7.39	26.72
Ferry-Port on Craig	46.36	31.17	49.49	0.81	62.35
Flisk	107.79	66.90	141.80	0.00	68.42
Forgan	217.81	134.41	168.62	0.00	238.87
Kemback	138.87	55.57	108.20	0.00	0.20
Kennoway	181.98	117.31	184.72	1.62	36.03
Kettle	223.79	202.02	367.00	5.36	251.32
Kilconquhar	176.72	118.02	292.41	17.51	143.12
Kilmany	180.77	159.62	213.26	0.00	89.88
Kilrenny	214.37	111.74	167.11	2.83	17.00
Kingsbarns	257.89	102.83	143.32	5.16	0.00
Largo	284.41	150.61	243.93	0.30	166.60
Leuchars	420.55	215.38	410.12	0.00	439.78
Logie	162.45	93.02	155.97	0.00	156.48

Table 3.12 (continued)

Parish	x_5	x_6	x_7	x_8	x_9
Monimail & Moonzie	78.95	42.51	64.17	0.00	0.00
Newburgh & Scoonie	230.06	175.51	305.06	5.67	134.51
Newburn	91.09	62.75	97.57	2.43	160.32
Pittenweem	10.53	10.63	27.02	0.00	0.81
St. Andrews & St. Leonards	620.85	297.77	449.09	1.11	91.30

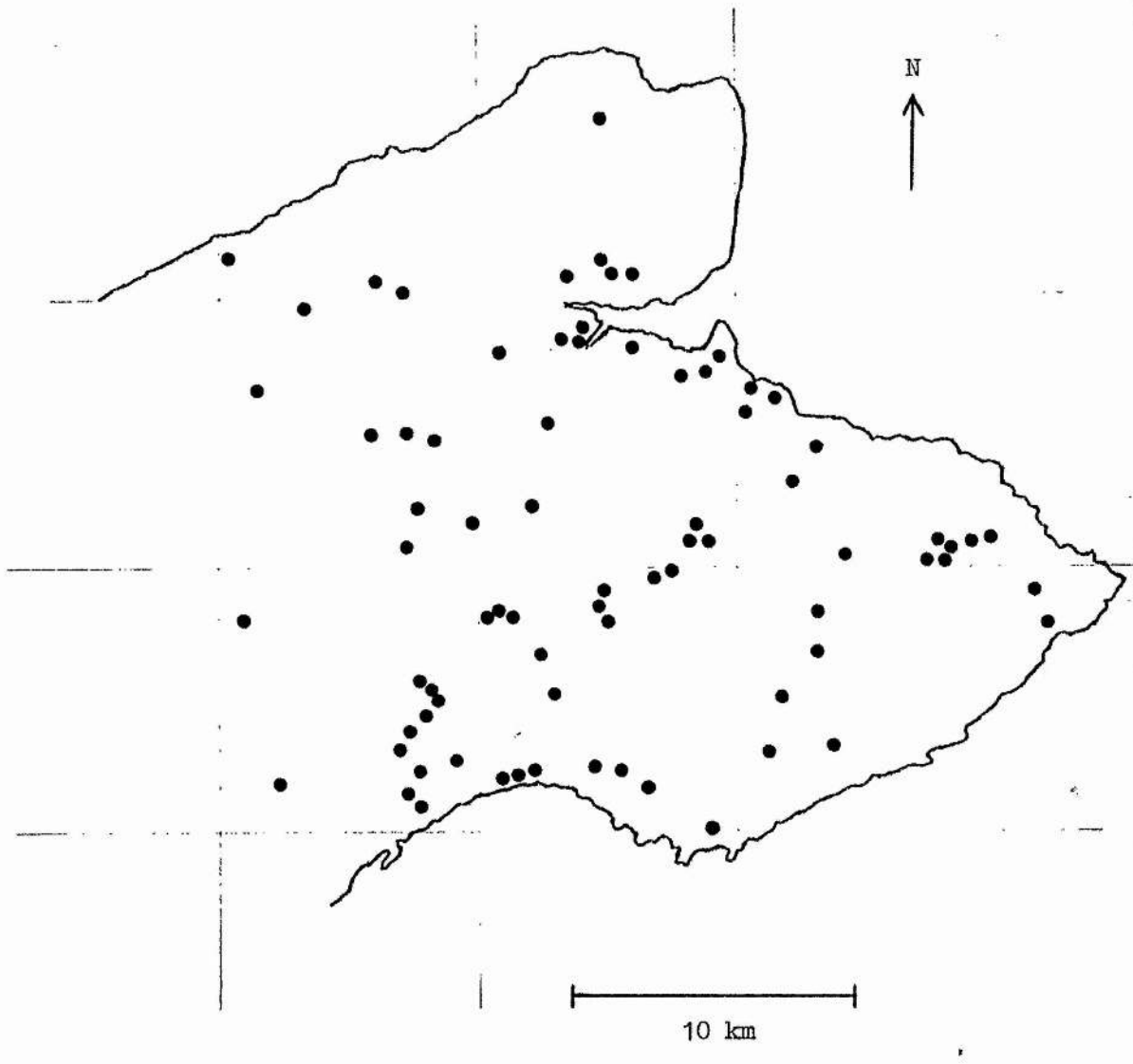


Fig. 3.1 The geographical distribution of N.E. Fife rookeries known to exist in 1978. The rookeries are aggregated.

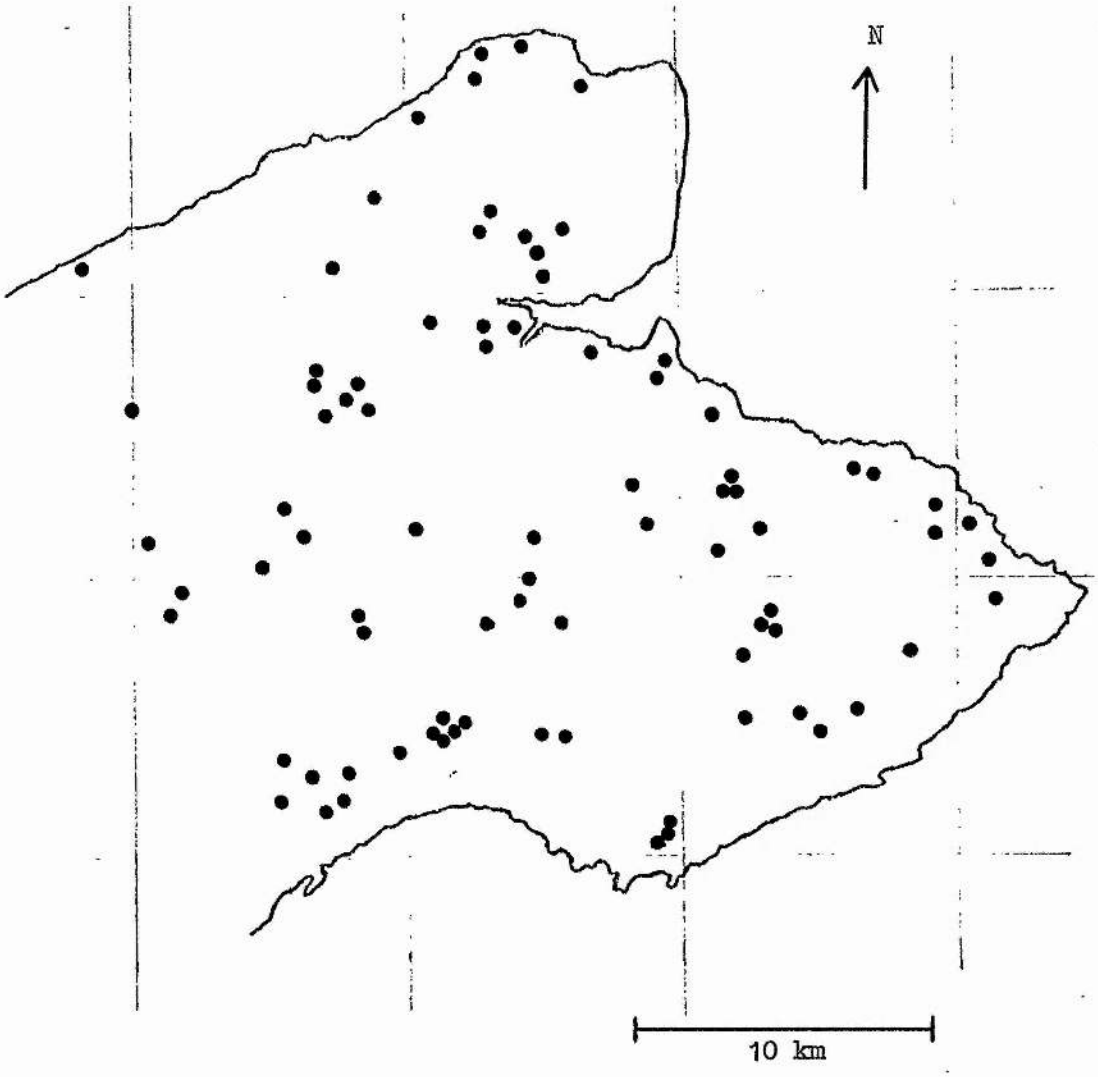


Fig. 3.2 The geographical distribution of N.E. Fife rookeries in 1945. The rookeries are randomly distributed.

Chapter 4. Habitat use by rooks and carrion crows

INTRODUCTION

The study of the use animals make of their habitats is an important area in ecology. Quite apart from the contribution it makes to a complete understanding of the life history of a study species it can be of immense value in highlighting general rules in areas of evolution such as speciation, fitness and dispersion to name but three.

Clearly, for an animal to survive and reproduce its choice of habitat will be crucial. The fittest individuals in a population will be those who are better adapted to the prevailing environmental and social conditions, and those who are ill-adapted will be less likely to leave surviving offspring. The problems facing animals in this respect, then, will be those of where and when to search for food, how long to search one part of the habitat before sampling another part for possible food items, when, where and how long to spend resting, preening, looking for a mate, etc. The solutions to these problems will vary with many factors including the broad nature of the available habitat, competition from other species, competition from conspecifics (which will depend on population density), geographical location, climatic factors and others. The same strategy for apportioning time to various activities or to feeding at various feeding stations within the habitat at one locality may not be the best strategy at another locality. Similarly, different animals may require different strategies due to phenotypic or genotypic differences between them, and even the same animal may be forced to adopt different strategies at different times of the year or under different meteorological conditions. The problems, then,

involved in choice of habitat and behaviour within that habitat seem to be awesome. In a relatively stable environment it may be most parsimonious for an organism to have a genetic predisposition to choose one habitat (or part of it) rather than another. In a more unpredictable environment it may be more advantageous to be more flexible in habitat choice and to learn from conspecifics which are the suitable characteristics of the habitat for inhabiting. Although there is no evidence to support these hypotheses it has been shown that habitat preference may be genetically determined (for example hand-reared blue tits Parus caeruleus prefer to perch on oak branches, whereas coal tits P. ater prefer pine branches, Partridge 1979). Of course learning processes are of great importance as well (Klopfer 1963).

With respect to corvids, questions such as these may also be of economic importance to man. In order to gauge the amount of damage caused by birds to crops it is necessary to know the pattern of habitat use by these birds. A previous study of rooks on agricultural land in Aberdeenshire was carried out specifically to answer this question (Dunnet & Patterson 1968, Feare 1974, Feare et al 1974). Other smaller, and therefore less comprehensive, studies have also considered the use made by rooks of certain field types in their habitat. Casual observations by Elton (1927) showed that a greater percentage of recently sown fields contained rooks than did pasture fields. Marples (1935), using a similar method to Elton (i.e. observing from a train), also found that proportionally more recently sown fields than grass ones contained feeding rooks, though if "rough grass" was included this was not the case. He also discovered proportionally more ploughed fields than grass or recently sown fields to have rooks in them. In winter only, however, did grass seem to be the most important field type for rooks. These

observations do not necessarily give a fair representation of the pattern of habitat use by rooks, though. Among the reasons for this are that few observations were made (one train journey for Elton and 15 for Marples), and that the actual numbers of rooks using fields were not counted (only the fields containing rooks were).

In the investigation carried out for the Ministry of Agriculture and Fisheries from 1944-1946 into the population and feeding habits of the rook (see chapter 2) Fisher (1948) reported that actual numbers of rooks counted on grass fields during the course of the year greatly exceeded those in other types of field, notably those sown with cereal. More rooks were seen ".... on fields or in places where any grain eaten might be a loss" than on stubble fields. Again, this presented no clearly defined pattern of use of the whole habitat for feeding by rooks. Lockie (1955) also reported grass to be the predominant field type used by rooks in Oxfordshire though he gives no figures. In New Zealand, Purchas (1980) has also identified grass fields as being important for rooks throughout the year for capturing invertebrates.

Comparable estimates to the above studies of the proportions of birds seen feeding on grass fields (i.e. about 50% throughout the year) were obtained by Feare (1978) for Hampshire rooks. Feare (1978) compared the use rooks made of various field types in Hampshire with similar data from the Aberdeenshire study (Dunnet & Patterson 1968, Feare 1974, Feare et al 1974). He found grass to be used more in Hampshire than in Aberdeenshire at most times of the year, but especially in the winter months. Other important utilised field types in these two localities were ploughed land, braird, potatoes and other crops, all when available. The temporal availability of field types in some cases differed between the two study areas, so the importance of them to rooks at different

times of the year also differed. This was most marked with respect to stubble fields, which, when available, were heavily utilised by rooks. Differences in the dates of sowing as well as the number of sowings resulted in a greater availability of stubble in Aberdeenshire. Differences in farming practice between the two counties accounted for differential use by rooks of stubble in particular, and all crops generally.

Comparable studies of the habitat use of the carrion crow have not been as intensively undertaken as those on rooks, due partly no doubt to the carrion crow's lesser standing as a pest of agricultural crops. On a more global level than the rook studies referred to above, Loman (1980b) has compared the two species' (as well as the jackdaw's and magpie's Pica pica) winter use of grass habitats in Sweden. These comprised about 80% of the available habitat of his study area and were classified as "dry", "moist" or "intermediate". He found that in early and late winter rooks preferred intermediate habitat, as did carrion crows, but the latter also showed a preference for moist over dry meadows in late winter.

At this point a note on the use of the term 'habitat' is pertinent. Confusion has arisen in the past over the terms habitat and niche (and others). Whittaker et al (1973) attempted to standardise the use of these terms. They restrict the term 'niche' to refer to the intracommunity role of a species. That is, the niche of a species is defined in terms of the functional attributes of that species within an ecological community. Habitat, on the other hand, they define in terms of intercommunity attributes, being the way a species distributes itself in the environment in response to environmental variables. They further define ecotype as the whole range of environmental factors impinging on a species. A further distinction made is that between biotope and habitat. Biotope

should, they state, refer to a community's environment, whereas habitat should refer to the environment of a species. This formulation has been criticised by Kulesza (1975) because niche and habitat variables may not strictly be dichotomous classes. Whittaker et al (1975), though, recognise that certain variables, e.g. temperature, may be components of niche or habitat. I here use the term habitat, then, as defined by Whittaker et al (1973, 1975). The relationships between rooks and carrion crows with respect to habitat use, being a component of the niches of the two species, will, as already mentioned, be considered more fully in the following chapter.

The present chapter, then, aims at describing the daily and seasonal pattern of the use made by rooks and carrion crows of their habitat for feeding and other purposes. Differences and similarities between the two species in these respects are noted, as they are between successive years where this information is available. Comparisons of the habitat use of more than one species are an important preliminary step in studies of competition between these species. If two species show great overlap in their use of the same habitat this does not necessarily mean that they are competing with each other. It is more likely that they are ecologically separated in another way, such as feeding on different foods. Observed overlap does point to the possibility, however, that the species may be competing, either actively (interference competition) or passively (exploitation competition). Though overlap between the two species under consideration here is touched upon in this chapter more precise quantification of the extent of this is given treatment in the chapter which follows this one.

METHODS

From September 6, 1977 to February 27, 1979 I made 427 journeys, usually by public transport, between Guardbridge and St. Andrews. This is a distance of 5.5 km, and from the road 5 rookeries are visible (see Fig. 4.1, p. 184). The land surrounding the road is almost exclusively farmland. All fields on the route (and therefore all crop/substrate types) are divided from each other by fences, hedges or walls. The fields on the north side of the road are demarcated by the River Eden estuary for most of the length of the road but by golf courses at the eastern end. The area visible on the south side of the road is defined by the brow of a bank, along part of which there are trees. During each trip I recorded (usually on paper but sometimes on tape) the numbers and locations of all rooks and carrion crows I observed. I also scored the activity of these birds with respect to three categories. These were:

Flying. Birds in flight could be so either 'in rookery' - i.e. flying within approximately 25m of a rookery, or actually flying within it or above it, or in flight elsewhere.

Resting. This included birds which were perched on walls, wires, etc. and also birds which were observed preening. Also included were those birds in fields which were inactive, i.e. not moving and not exhibiting any obvious signs of feeding or foraging.

Feeding. All birds in fields which were observed pecking the ground were scored as feeding. Those which were walking were assumed to be engaged in feeding related activities such as searching for food. Birds which were looking up were also recorded as feeding as they were assumed to be looking up temporarily between foraging sequences.

In addition to numbers and activities of birds I also noted

the crop/substrate type that they were on during resting or feeding. Several of these were well represented along the route and included, at varying times of the year, the following:

Grass. Usually permanent pasture.

Plough. Land ploughed usually after the harvesting season in late summer. If ploughing was actually in progress during a transect count then this was noted and scored separately.

Stubble. This was always barley, and consists of the cut stalks of the plant protruding usually up to about 20cm above ground level.

Potatoes. Newly planted or recently harvested.

Sown Barley. Newly planted, ungerminated seeds.

Braird. Again, always barley, recently germinated and not over 15cm in height.

Dung. This could either be heaps of straw mixed with cow dung in fields or whole fields on which this had been scattered. The mixture of straw and dung results from cow sheds being cleaned out.

Mud. This consisted of mudflats on the River Eden which were available to birds to forage on as tides dictated.

Waste. This included gravel areas and paths, roads, sand pits, dustbins, etc. - broadly, areas where birds scavenged for food.

Smaller areas of the following were also available for parts or all of the year:

Fallow. Bare soil with nothing planted on it, being 'rested' for planting the following season.

Sown grass. Newly planted grass, not a cereal crop.

Various other potential feeding stations were available or utilised unpredictably. These were animal feeding troughs, trees, stacks, and even one rook was seen making swallowing movements after

pecking the back of a sheep on which it was perched.

Crops which were not available along the transect route from 1977-1979 included oats, wheat and root vegetables. Fields of these have been used for foraging by rooks in other studies (e.g. Feare et al 1974) and may have been used by rooks outside the transect area in this study.

Routine data on the weather as well as time of day and date were always noted.

Each field or discrete piece of ground was monitored throughout the study for crop changes. These changes usually followed predictable courses, e.g. sown barley was always followed by braird, followed by the well established crop, then stubble, and then (usually) dung followed by plough. Figures 4.2-4.5 (pp. 185-188) show changes in crop/substrate types that occurred in each field between September 1977 and February 1979.

The numbers of birds in large flocks could usually not be assessed exactly. In these cases the total number of birds present had to be estimated. This was achieved by counting ten individuals, noting the approximate area these occupied and extrapolating from this to the total area occupied by the whole flock. It is unlikely that gross errors would have been made using this method, and the occasions when I had the chance to count all individuals in a flock and compare the result with the estimation method figure then there was never an error greater than 10% in either direction. Feasibly with very large flocks the error could have been greater but these were relatively infrequently observed.

Another possible source of error was in failing to spot carrion crows in the midst of a flock of rooks. It is not known how often this might have happened, but it is unlikely to have occurred very often, if at all, in conditions of good visibility (which did

not usually coincide with extremely large winter rook flocks, however). Usually, the two species were seen feeding, resting or flying separately.

At certain times of the year, especially those when trees were in full leaf, it could be impossible to assess with any accuracy the numbers of rooks perched or flying in rookeries, so some counts of rooks in these months will be underestimates.

No observations were made if part or all of the area normally visible was obscured for some reason, e.g. haar, fog, poor light.

RESULTS

A total of 427 transect counts were made during the course of this part of the study, but carrion crow data were not available for September 1977 or from November 1977 to February 1978 inclusive. Table 4.1 (p. 163) gives a breakdown by month and time of day of these. The total numbers of rooks and carrion crows seen during these counts are given in Tables 4.2 (p. 164) and 4.3 (p. 165) respectively.

The average number of rooks and carrion crows seen per transect count in each month of the study are plotted in Fig. 4.6 (p. 189). From December 1977 to August 1978 rook numbers remained fairly stable having declined from a peak in September 1977. After August 1978 there was another rise in rook numbers and this remained high, having subsequently fluctuated, until February 1979.

Figure 4.7 (p. 190) portrays the average numbers of rooks seen per transect at various times of the day in the different months of the study. There is no difference in numbers seen per count between the months though there was a trend for more rooks to be seen

in the autumn and winter months (Friedman two-way analysis of variance, $X_r^2 = 24.74$, 17 df, $0.2 > p > 0.1$). Similarly, there is no difference between times of day with respect to the number of rooks seen per transect ($X_r^2 = 4.95$, 3 df, $0.2 > p > 0.1$) though again there is a trend for fewer rooks to be seen in the mornings and late afternoons than in the early afternoons and evenings.

Carrion crow numbers were stable at around just over two birds per count for most months, though there were deviations from this number in April and November 1978 and February 1979. Figure 4.8 (p. 191) shows similar data for the carrion crow as is presented in Fig. 4.7 (p. 190) for the rook. There are no differences in the numbers of carrion crows seen per transect at different times of the day ($X_r^2 = 3.12$, 3 df, $0.5 > p > 0.3$). No significant differences emerged either in the numbers of crows seen in different months ($X_r^2 = 8.86$, 12 df, $0.8 > p > 0.7$).

For some months data are available from two successive years. These are October in 1977 and 1978 for carrion crows, and September to February 1977/78 and 1978/79 for rooks. The proportions of both species engaged in the different activities and feeding in the various field types which were available in the same months in successive years mostly differed (in some cases highly significantly so) but the distribution of the number of transects taken at different times of the day were not correlated, making statistical comparisons between these months spurious. An exception, however, was October, where the number of transects taken within three hour intervals throughout the day in 1977 and 1978 were correlated ($r = 0.96$, 4 df, $p < 0.01$). Only the statistical treatment applied to successive Octobers, then, have been noted in the following summaries of gross activity and of the use of resource stations by the two species. Comparisons were made using the chi square test (Siegel

1956). The proportions of resting/rookery/feeding birds recorded in October 1977 were compared with the proportions engaged in these activities in October 1978. Similarly, the proportions of feeding birds recorded feeding on grass/stubble/waste in October 1977 were compared with the proportions of feeding birds feeding on these in October 1978. Grass and stubble were used by rooks and crows in both Octobers, and rooks also used waste ground in both years.

Resting birds

Figure 4.9 (p. 192) shows the percentages of total numbers of rooks and carrion crows observed which were resting. Clearly the pattern for each is different. Generally, low percentages of rooks resting coincide with high percentages of carrion crows resting. The highest proportions of resting rooks occurred in October 1977 (22.49%) and September and October 1978 (18.87% and 17.45%). Carrion crow peaks of resting occurred in July, November and December 1978 (21.74%, 26.79% and 26.67%) however. Low proportions of birds resting were recorded for both species in April and May 1978 and February 1979.

The proportion of crows resting in October 1978 was 11.9% whereas no crows were observed resting in the previous October. Significantly more rooks were observed resting in October 1977 than in October 1978 ($X^2 = 233.86$, 1 d.f., $p < 0.001$).

Rookery attendance

The numbers of rooks counted in rookeries probably included some which were resting also. In Fig. 4.10 (p. 193) the percentages of all rooks seen which were perched in a rookery are portrayed. From low proportions in September and October 1977 the rookery sites gradually came to contain a greater percentage of rooks seen, peaking

in May 1978 when most of the birds observed were in a rookery (51.78%). Gradually again this declined to less than 1% in July 1978. There was a small peak also in December 1978 (18.79%) before declining again. A difference emerged between the proportions of rooks in rookeries in the months of January and February between 1978 and 1979 (29.81% and 26.05% vs. 9.29% and 8.14%). There was also a significant difference between October 1977 and October 1978 in the number of rooks seen in rookeries (0.03% and 1.25% respectively, X^2 = 42.85, 1 d.f., $p < 0.001$).

Feeding birds

Tables 4.4 (p. 166) and 4.5 (p. 167) show the numbers of rooks and carrion crows observed which were feeding or foraging, and Fig. 4.11 (p. 194) displays these as percentages of the total numbers of birds seen of each species.

Generally high proportions (100% in May 1978) of carrion crows seen each month were feeding. Only from May to August 1978 and in December 1978 was the percentage of crows seen feeding less than the percentage of rooks seen feeding, and only in December 1978 did the percentage of crows seen feeding drop below 50%. In October 1977 and October 1978 (October being the only month from which carrion crow data were available from different years) the proportion of crows seen feeding differed considerably, being 95.6% and 69.05% respectively (X^2 = 15.88, 1 d.f., $p < 0.001$; Fig. 4.11, p. 194). There is no correlation between the numbers of carrion crows seen feeding each month and the numbers which were not feeding ($r = 0.24$, 11 df, $p > 0.05$). In other words, the proportion of crows which were feeding in each month varied, the number feeding being independent of the number which were not feeding.

The proportions of rooks seen which were feeding also was

fairly high throughout the year, though in a few months it fell to below 50% with a low (20.39%) in March 1978. Highest percentages were obtained from June to August 1978. Months in which data were obtained in different years, viz. September to February 1977/78 and 1978/79, show varying proportions of feeding rooks, and also a different pattern in these figures over this time. In 1977/78 the overall pattern was a decrease in the proportion of rooks seen which were feeding whereas in 1978/79 the pattern over these months was an increase (Fig. 4.11, p. 194). There was a significant difference between successive Octobers here, with proportionally more rooks feeding in October 1977 ($X^2 = 4.86$, 1 d.f., $p < 0.05$). In contrast to carrion crows, there is a correlation between the numbers of rooks feeding and the numbers not feeding in each month ($r = 0.57$, 16 df, $p < 0.02$), indicating that the proportion of rooks seen feeding in each month remained roughly constant.

The proportions of rooks seen which were feeding in each month and at different times of the day, however, are plotted in Fig. 4.12 (p. 195). The proportions seen feeding in different months differed significantly (Friedman two-way analysis of variance, $X_r^2 = 45.93$, 17 df, $p < 0.001$), with higher proportions generally occurring in the summer months, and lower proportions in autumn and winter. Similarly, the proportions seen feeding at different times of the day differed significantly ($X_r^2 = 24.12$, 3 df, $p < 0.001$), more rooks feeding in the earlier half of the day than in the latter half.

Figure 4.13 (p. 196) shows similar data for the carrion crow as is presented for the rook in Fig. 4.12 (p. 195). There were no differences in the proportions of carrion crows seen feeding at different times of the day ($X_r^2 = 2.47$, 3 df, $0.5 > p > 0.3$), and only a trend for there to be more feeding at certain times of the year (notably winter and spring: $X_{r2} = 16.73$, 12 df, $0.2 > p > 0.1$).

Table 4.6 (pp. 168-169) shows the average size of feeding flocks of rooks at different times of the day for the duration of the study. There were no significant differences in the mean feeding flock size either throughout the day (X_r^2 4.82, 3 df, $0.2 > p > 0.1$) or over the months ($X_r^2 = 21.15$, 17 df, $0.3 > p > 0.2$). Flocks did tend to be larger, however, in autumn and winter.

Table 4.9 (p. 172) shows the total numbers of rooks and carrion crows which were observed feeding or foraging at each foraging station represented along the transect route. Tables 4.10 to 4.14 (pp. 173-177) show a breakdown by month of these data, and Figs. 4.14 (p. 197), 4.16 (p. 199) and 4.18 to 4.20 (pp. 201-203) express the data for some of the foraging stations as percentages of the total number of each species seen feeding.

Grass. Figure 4.14 (p. 197) shows that during the course of a year both rooks and carrion crows utilise grass for feeding purposes to large extents. Indeed, most feeding rooks in the summer months were observed on grass, though lower proportions were recorded in September 1978. Even in the winter high proportions of rooks use grass for foraging. The periods when fewer rooks used grass were late winter/spring 1978 and autumn 1978. There is a difference between years, with higher proportions of feeding rooks on grass in September and October 1977 than in the same months in 1978 (for Octobers, $X^2 = 137.08$, 1 d.f., $p < 0.001$). Even in November 1977 and 1978 there remains a difference with the higher proportion in this month being recorded in 1978 this time. In January and February 1978 lower percentages were scored than in the same months in 1979.

Figure 4.15 (p. 198) depicts the mean flock sizes of rooks observed feeding on grass at the various times of the day and year. There was no difference in mean flock size from month to month (X_r^2 =

23.81, 17 df, $0.2 > p > 0.1$), but there was at different times of the day ($X_r^2 = 11.00$, 3 df, $p < 0.02$), feeding flock size on grass being higher in early afternoon and evenings. Flock size on grass also tended to be higher in autumn and winter. Table 4.7 (p. 170) shows the overall mean flock sizes on grass for times of day and year. These figures show a similar pattern to those for all foraging stations combined (Table 4.6, pp. 168-169).

The pattern of use of grass for foraging by carrion crows is similar to that by rooks in that it too fluctuates around a peak in the summer. There is here, however, a more clear general trend in that carrion crows' use of grass begins to rise in spring, peak in summer and fall gradually away again in winter. There was also a difference between years as the proportions seen feeding on grass in October 1977 and October 1978 were 12.64% and 58.62% respectively ($X^2 = 22.66$, 1 d.f., $p < 0.001$).

Stubble. Figure 4.16 (p. 199) shows that during autumn and winter barley stubble is an important foraging station for rooks. Most rooks seen feeding in February, September and October 1978 (72.42%, 71.03% and 61.61%) were doing so on this type of field. Smaller percentages of carrion crows were also recorded feeding on stubble, and, in fact, in December 1978 carrion crows continued to utilise stubble fields whereas rooks had ceased to do so. Worthy of note again is the difference between years, especially in successive Octobers, in the proportion of birds using stubble. In October 1977 34.32% of feeding rooks and 82.76% of feeding carrion crows were on stubble, whereas in October 1978 the respective proportions were 61.61% ($X^2 = 239.37$, 1 d.f., $p < 0.001$) and 6.9% ($X^2 = 50.96$, 1 d.f., $p < 0.001$).

The average feeding flock size of rooks on stubble in the

months that it was available and utilised by them are shown in Fig. 4.17 (p. 200). No significant differences emerged with respect to time of day ($X_r^2 = 0.52$, 3 df, $p > 0.05$) or year ($X_r^2 = 15.60$, 10 df, $0.2 > p > 0.1$). Overall flock size means for rooks feeding in stubble fields at different times of the day and year are shown in Table 4.8 (p. 171).

A comparison between the mean sizes of rook flocks feeding on grass and on stubble, matched for time of day and month, and for only those months when grass and stubble were available and used by rooks (i.e. September 1977 - March 1978 and August - November 1978) revealed that flocks which fed on stubble were significantly larger than those which fed on grass (mean flock size for grass fields = 10.97, s.d. = 20.53; for stubble fields = 18.87, s.d. = 22.84: $t = 2.55$, 43 df, $p < 0.05$). Barley. The percentages of feeding birds observed on sown barley and braird are shown in Fig. 4.18 (p. 201). As can be seen both rooks and carrion crows utilise these field types to a large extent when they are available (generally sown barley in March/April and braird in May/June).

From the road it could be difficult to see if birds were feeding on lodged barley when this was available. It is unlikely, though, that this was an important feeding station for two reasons: 1) areas of lodged barley were small in 1978; and 2) birds were rarely seen flying low over barley fields in the summer.

Plough. When ploughed land is available it also is an important foraging station for rooks and carrion crows. The pattern of use as shown in Fig. 4.19 (p. 202) is similar for both species, and even seems to be similar for both years in the case of the rook. The summer months are those when plough is used least for foraging by

rooks and crows, and the two highest proportions of feeding rooks seen on ploughed fields occurred in December 1977 and 1978 (28.11% and 33.63%). Crows were never observed feeding on a field when there was a tractor present in the process of ploughing it.

Dung. Figure 4.20 (p. 203) reveals that high proportions of feeding carrion crows and rooks use cow dung for foraging on at certain times of the year. This includes both dung covered stubble fields and dung heaps. Though rooks did not use dung heaps within the transect area they did use them elsewhere.

Again, there seemed to be a difference with respect to rook utilisation of dung covered stubble between 1978 and 1979. In January and February 1978 the proportion of feeding rooks seen on this type of foraging station were 0% and 7.34%, whereas in 1979 in the same months the respective figures were 51.09% and 20.11%. A similar comparison cannot be made for carrion crows but it is worth noting that the proportion of feeding crows on dung covered stubble in March 1978 was as high as 47.17%, whereas in January and February 1979 the proportions were only 25% and 13.79%.

In the summer months of 1978 carrion crows utilised dung heaps. This began with a high proportion in June (27.78%) and dropped dramatically thereafter to low proportions throughout July, August and September (all < 3%).

Potatoes. Table 4.13 (p. 176) shows that when potatoes were planted in one field in May 1978 a total of 21 rooks used the field for foraging on. This represents a small percentage (2.10%) of the birds observed feeding in that month. In the following month 38 rooks (3.43% of feeding birds) used the field. When the potatoes had been harvested in September 1978 the percentage of rooks using the field dropped to .....

1.99% (17 birds) in that month, and 1.13% (14 birds) in October 1978 (Table 4.12, p. 175).

Carrion crows used this field also to about the same extent (2.74%, 3.70% and 2.94% in May, June and September 1978 respectively, each proportion representing two birds; Tables 4.13 and 4.12, pp. 176 and 175).

Waste. In December 1977 the highest proportion of feeding rooks on waste ground was recorded (10.81%). This represents 20 birds, 18 of which were being provisioned with scraps by an old man. In most months, though, only around 1-3% of feeding birds did so on waste ground. There was a difference between successive Octobers though, proportionally more rooks feeding on waste ground in October 1978 than October 1977 ($X^2 = 27.06$, 1 d.f., $p < 0.001$).

Carrion crows, by contrast, used roads, etc. proportionally more often, and in two months, October and November 1978, more than 10% of feeding crows were on this type of foraging station (13.79% and 10.34% respectively; Table 4.12, p. 175).

Mudflats. Rooks were never seen foraging on the intertidal mud at the mouth of the River Eden at Guardbridge. Carrion crows, on the other hand, did so in several months. Notably, in September 1978 and to some extent in October 1978 high percentages of crows were observed foraging on the estuary bed (36.76%, 25 birds and 17.24%, 5 birds respectively; Table 4.13, p. 176).

Fallow. Carrion crows were never observed foraging on fallow ground but rooks used it to a small extent in September and October 1977 (0.67%, 17 birds and 0.36%, 8 birds respectively; Table 4.13, p. 176).

Sown grass. Rooks used a sown grass field when it was briefly available in November 1977 (80 birds, 27.87% of those seen foraging that month; Table 4.14, p. 177). Seven carrion crows were observed foraging on a different sown grass field in June 1978, but this was not used by rooks.

Other foraging stations. Table 4.14 (p. 177) shows the numbers of rooks and carrion crows which foraged on other, less abundant foraging stations. Clearly, stacks, trees, a sheep's back and animal feeding troughs were not important places for gathering food for either species.

Figures 4.21 and 4.22 (pp. 204 and 205) summarise the monthly activity and feeding patterns of the two species and portray additional data for resource stations which were used infrequently and which have not been depicted eleswhere.

In addition to the patterns of activity and feeding by rooks and crows described above I compared the difference in use of the same foraging stations within months by the two species. For each field type that was used by both species (rarely together in mixed species flocks) in each month the proportions of feeding rooks using it were compared with the corresponding proportion of feeding crows.

Both species used grass fields for foraging in all months, but the proportions of each doing so differed significantly in most months. Rooks used grass to a greater extent than crows did in all of these months except September and October 1978, when proportionally more crows than rooks were observed foraging on grass. The months in which there were no differences in the use of grass fields were April, May, August and November 1978.

In the months when rooks and crows both foraged on stubble fields they did so to significantly different extents. In September and October 1978 proportionally more feeding rooks than crows were on stubble, whereas in October 1977 crows used stubble more intensively.

In the month when proportionally more rooks used ploughed fields for foraging (October 1977) the difference was not significant. When proportionally more crows than rooks foraged on this type of field (January and February 1979), however, the difference was large but the rules for chi square were violated.

In January 1979 rooks made significantly heavier use of dung-covered stubble fields than crows. This was reversed (but not significtly) in February 1979 when crows foraged on them to a larger degree.

When sown barley was abundantly available rooks used it more intensively in March 1978, but in the following month proportionally more crows foraged on it.

In all months when both crows and rooks foraged on waste ground the former species did so to a greater extent but the numbers involved were too few for proper analysis.

Table 4.15 (pp. 178-179) summarises these comparisons.

Table 4.16 (p. 180) lists the field types which were used by one species but not the other in each month. Interestingly, in four months rooks used waste ground when crows did not, as opposed to only two months when crows foraged on it when rooks did not. In months when crows foraged on dung, rooks did not. Also, as mentioned earlier (see Table 4.9, p. 172), certain resource stations were not used by one species. Only in October 1977 and March 1978 did crows not have exclusive use of some field types, and similarly in January and February 1979 rooks did not have exclusive use of some.

From Tables 4.15 and 4.16 (pp. 178-180) it is clear that

rooks and carrion crows differed considerably in their use of the habitat for foraging.

DISCUSSION

Rook numbers

There was a general trend for greater numbers of rooks to be recorded in the autumn and winter months, and also for feeding flocks to be larger at this time. It is unlikely, though the possibility cannot be ruled out, that this was due to an influx of migrating birds from Europe. European rooks are not known to spend the winter in this part of Britain (Busse 1969), though a rook hatched in Finland in 1976 was recovered in the spring of 1977 in N.E. Fife (Spencer & Hudson 1978). The reason could simply be that the total population size had been boosted by young birds produced in the breeding season. The data are certainly consistent with the pattern in Aberdeenshire for young rooks to undertake seasonal movements (Dunnet et al 1969). The nature of these in Aberdeenshire, where circumstantially there were (local?) migrations into the study area in autumn and emigration from the study area in summer, are approximately mirrored by the numbers of rooks observed at these times in the present study (see Fig. 4.6, p. 189). An influx of rooks in springtime was recorded in the Aberdeen study but not in this one. The discrepancy between the numbers observed after breeding in 1978 and those in autumn 1978 (October) suggest that it may not only be the birds resident in the five rookeries along the transect route which were involved in these movements, if, indeed, dispersal is the reason for the difference. Local migration could be taking place over a much wider area and involving many rookeries.

Such movements, concerning not only young birds certainly take place elsewhere in Scotland. McKilligan (1980), for example, recorded daily movements of rooks covering a distance of up to 45 km and back in Deeside in winter (i.e. November-February). Patterson et al (1971) record Aberdeenshire rooks as returning daily to the rookery grounds from the winter roost to feed - a distance of 16 km. There have been many more local studies on rook movements in winter to and from roosts (see, for example, Stewart 1924, Harrisson 1932, Brian & Brian 1949, Burns 1957, Coombs 1961), and these have involved movement up to a distance of 32 km. Large numbers of rooks may account for some of these movements. For example, in the winters of 1963 and 1964 in N.E. Fife 20,000-30,000 rooks and jackdaws were observed flying to roost (Editor, Scottish Birds 1964, 1965). Much greater distances may be travelled by European rooks on migration, of course (Busse 1969), but these can hardly be termed local movements. In any event, this small scale dispersal to and from roosts and rookeries does not explain the influx of birds to an area, only movements within it.

Strathtyrum (rookery 41/06) functioned as a winter roost for rooks. The nearest recorded winter roost outside the St. Andrews - Guardbridge route was at Kirktonbarns (rookery 42/01), 6.5 km away. Presumably rooks from other parts of N.E. Fife nearer to Strathtyrum than Kirktonbarns also moved in for at least winter roosting in the Strathtyrum roost. The times at which transect counts were made in winter, however, were not biased towards those times when pre- or post-roosting flocks of rooks were likely to be encountered (Table 4.1, p. 163), so the data do not represent birds which were involved only in local movements at roosting times.

A likely explanation of the increased numbers of rooks observed in winter is that flocks of young birds from a wide area had

moved into the transect area, as suggested by Dunnet et al (1969) in Aberdeenshire. Holyoak (1971) noted the somewhat nomadic tendencies of such flocks. The pattern presented here could be spurious, however, as many of the counts made in spring and autumn/winter were underestimates. Considering the magnitude of the difference in numbers seen, though, this is probably unlikely. There were, however, no occasions when I recorded a flock made up entirely of "black-face young". Not only young birds might be responsible for migration into the area in winter. Another possible explanation of greater rook numbers in winter is that there could have been fewer birds feeding near their rookeries in the summer months. Aberdeenshire rooks certainly feed further from their nesting quarters in the summer (Dunnet & Patterson 1968, Patterson et al 1971).

That fewer rooks were seen in the mornings and late afternoons is probably accounted for by the fact that any rooks present at these times were less conspicuous. Those were times when smaller proportions of rooks were seen feeding (see Fig. 4.12, p. 195). When they were not feeding they must have been flying or resting, which could have resulted in them being overlooked or out of sight during transect counts. Low proportions were also recorded feeding in the evening, but rooks were generally more conspicuous in the evenings as they were preparing to roost.

General activity of rooks

The predominant activity rooks engaged in throughout the year was feeding. They spent less, and also a less variable amount of, time from month to month flying. Even less time was spent resting and rookery attendance varied considerably throughout the

months of the study.

The time at which rookery attendance was highest was, not surprisingly, during the breeding season. This was most marked in March when nest-building began. Numbers observed in April and May, while still high, were underestimates due to the difficulty of seeing females on the nest, and also young when they had left it and were sitting on nearby branches. Attendance at the rookeries was also fairly high after the summer. This is due to the fact that, of the five rookeries included in the transect route, two at least (Strathtyrum 41/06 and Cupar Junction 41/14) were used as autumn roosts by rooks. Strathtyrum also, as mentioned above, was a large winter rook roost. Of the other three rookeries neither Kincaple (41/05) nor Strathtyrum Lodge (41/15) was seen to be occupied by roosting rooks in the autumn or winter, and Golf Course (41/16; pine trees) probably did not function as a post-breeding roost as no birds were seen flying to it, or above it, at roosting times. The Strathtyrum roost attracted many birds from the surrounding area, and as a result of its proximity to Golf Course (0.6 km) the latter may have been less favourable as a roosting site, either because of its size (much smaller than Strathtyrum) or because of social factors. Rook roosts in winter do tend to be spaced widely apart, ranging from 8-12 miles (12.8-19.2 km) apart in Aberdeenshire and up to 16 miles (25.6 km) apart in southern Scotland. Some, however, are less than 5 miles (8 km) apart (Munro 1970, 1971, 1975; see also Patterson et al 1971).

The proportion of their time that rooks spent resting (including preening) varied from month to month during the study. From March to May very little time was spent resting due, no doubt, to the demands imposed on the birds by nest-building and other breeding duties. Of course, females on the nest have plenty time to

rest while incubating and brooding, but as these birds were rarely observed most of the observations at this time refer to males. These obviously have little time to devote to resting as they have to provide their mate with food at the nest and also feed themselves. After the breeding season (i.e. when the young have left the nest and also the rookery in June/July) birds could afford to rest more often in the fields. In the autumn of 1978, and also to some extent in the previous year, the time spent resting reached its highest levels as it did in Aberdeenshire (Feare et al 1974). In winter, especially that of 1978/79, rooks spent little time resting in the fields. This could be because they spent more time in the rookeries. These findings are roughly the same as those found in New Zealand by Purchas (1980), though rooks there rested more in the winter than did Fife rooks.

If food is short in winter time then it may be more advantageous for a rook to rest and/or preen in the rookery than in the fields, whereas if food is plentiful then it might pay to rest in the fields in between bouts of feeding, so saving energy by not flying to the rookery to rest. An equally, perhaps more, likely explanation is that birds are able to spend more time resting in the comparative safety of the rookeries in the winter because there is no shortage of food at this time. Clearly there need be no direct and clear relationship between time spent feeding and the amount of food available to be exploited.

If food is in short supply then the amount of time spent looking for food patches (and these might be evidenced by flocks already feeding on them) should be greater than when food is plentiful, and so the time spent flying around looking for food patches should be greater. The proportion of time spent flying was remarkably constant from month to month (as it was in New Zealand,

Purchas 1980), ranging from 5.37% to 36.5% with a standard deviation of only 8.2%. These proportions, though, are really made up of two categories of flying rook - those flying above or within 25m of a rookery, and those flying greater than 25m from a rookery. The latter were thus more likely to have been flying around, or looking for, feeding grounds or other feeding birds, whereas the former were less likely to have been engaged in food patch finding behaviour. Figure 4.23 (p. 206) reveals that the greater amounts of time spent flying when not near a rookery (i.e. over fields) occurred in the winter, particularly in 1978/79. This was also the time, however, when the lowest proportions of this category of bird were recorded. The peaks of flying over fields coincided with troughs of flying in the rookery, and vice versa, in this winter also. This suggests, if there is a relationship between the food supply and the time spent flying over fields, that food availability in the winter was unpredictable and also that it varied considerably. Patterson (1970) suggested that food in winter in Aberdeenshire was indeed localised. Most birds seen in the summer were feeding, and flying over fields at this time was at a minimum level, so perhaps birds had less difficulty in finding the available food in the summer. However, as no measure of food availability was taken during this study, it is not clear what the exact relationships are between times spent feeding and flying. Feare et al (1974) did estimate the amount of food available to rooks in Aberdeenshire throughout the year. They found that at different times of the year food availability was either high (in the breeding season and in autumn), moderate (in winter) or low (in summer). At all times of the year Feare et al (1974) found that the proportion of birds observed to be flying was fairly constant, at similar levels to those in the present study. So the number of birds flying in the Aberdeenshire study was independent

of food availability (though it is unclear whether flying birds in Aberdeenshire included those flying in the immediate vicinity of the rookery). The numbers of birds scored as feeding in Feare et al's (1974) study, however, generally reached their highest levels in summer when food availability was low, moderate levels when food was moderately available and lower levels when food abundance was high. This was roughly the pattern recorded by Purchas (1980) also. So, in parts of New Zealand and in Aberdeenshire at least, there seemed to be an inverse relationship between food availability and the number of birds which were feeding - apparently rooks devote more time to feeding, or rather searching for food, when food is in short supply. Moller (1982) also found that magpies in good quality territories (where food availability was also presumably high) spent less time feeding than magpies in less good territories. Applied to the present study, then, this would mean that food availability was at its lowest in the summer (as it is in Aberdeenshire) as this is when the greatest proportions of feeding birds were recorded (see Fig. 4.21, p. 204). If this is correct then it also means that when the food supply is low rooks are less likely to be seen flying over fields, preferring instead to forage on them despite the shortage of food. It seems that the birds are making a decision not to waste energy by flying around looking for other fields which will be no better (and could well be worse) in terms of food availability. Virtually all rooks seen foraging in the summer were doing so on grass (Fig. 4.14, p. 197), which was the most abundant field type in the study area throughout the year, and almost the only kind in the summer (see next chapter). So it does indeed seem that few birds were seen flying over fields in the summer because the other fields which were available were also grass ones and therefore as poor (or rich) in terms of food abundance and accessibility as the field on

which they were already foraging.

Fewest rooks were seen feeding in March 1978, clearly because at this time they were nest building and beginning to breed. Low proportions of feeding rooks were also recorded in the autumn and winter months, contrasting with the stated high proportions in summer (June-August) 1978. Food was probably in short supply at this time of the year. Grain was not available until harvest time in August, and during hot spells subsurface invertebrates either become more difficult to dig out as the ground gets harder (Feare et al 1974), live deeper (e.g. earthworms in the soil) or become otherwise less available, such as leatherjackets emerging into adult crane flies (Dunnet 1968, Dunnet & Patterson 1969). The demands on birds to feed, therefore, would have been greater in summer. This would have been especially so for young birds learning foraging techniques, but also for adults after breeding and with the imminent dietary requirements imposed by the moulting process. The overall pattern of feeding recorded in N.E. Fife was similar to that found in Aberdeenshire (Feare et al 1974).

Proportionally less rooks were observed feeding in the latter half of the day than in the earlier half, i.e. in mornings and early afternoons than in late afternoons and evenings. Again, this is roughly the same as Feare et al's (1974) observations in Aberdeenshire, and accords with other studies where birds feed particularly intensively in the morning shortly after roosting. Later in the day rooks presumably were more likely to have fulfilled their daily energy requirements and could devote more time to other essential activities such as preening and resting.

The size of feeding flocks of rooks tended to be larger, though not significantly so, in the autumn and winter months (Table 4.6, p. 168-169). Several, not necessarily mutually exclusive,

reasons probably account for this. First of all, there were simply more birds than usual in the area at this time (see above), and if they were roosting in the vicinity then it would have made sense for them to feed close to the roost also, providing food was available. Also, despite the availability of a greater variety of field types on which to feed in autumn and winter than in summer, good feeding stations may not have been evenly spaced throughout the study area and so the birds may have been congregating at the best ones. This should apply to flocks in the summer as well of course, but, as mentioned above, the best feeding stations viz. grass fields were more evenly dispersed in summer. The increase in rook flock sizes begins to become noticable after August (see Table 4.6, p. 168-169). This is when stubble fields were soon covered with dung, unlike the previous year when they were left untouched by farmers for several weeks. So farming practice also affects flock size at different times of the year, but it is worth noting that flock sizes on grass also are larger in autumn and winter (Table 4.7, p. 170, see below). So seasonal movements coupled with farming practice which affects the distribution of feeding stations may account for the observed seasonal variation of rook flock sizes. This again complements the findings of the Aberdeenshire study (Patterson et al 1971).

Use of the various feeding stations by rooks

By far the most common field type used by rooks for foraging throughout the study was grass. The rook's preference for grass fields is, of course, well documented. Since Fisher (1948) reported that in every month of the year rooks were observed in grass fields more often than in any other type of field several studies, including the present one, have confirmed grassland as being of

paramount importance to feeding rooks. In addition to the studies referred to earlier (i.e. Dunnet & Patterson 1968, Feare 1974, Feare et al 1974, Purchas 1980) which revealed grass as an important field type for feeding rooks, Coleman (1971), working on New Zealand rooks, deemed the rook to be a bird of pasture. Coleman's data, however, only show greater numbers of rooks on grass fields in the breeding season. There was, in fact, an avoidance of grass as suggested by his, and Dunnet & Patterson's (1968) index of utilisation of this field type, in winter. At other times high utilisation of cereal and other cultivated fields when they were available were seemingly preferred to grass. However, in the light of most studies of rook foraging in relation to available field types Lockie (1955) was probably correct in stating that "..... the rook is first and foremost a bird of grassland."

The reason for the rook's general preference for grassland is clear. Most of the animal matter ingested by rooks is found in grass fields. Lockie (1955) recorded 93% and 81% in 1952 and 1953 respectively of the volume of the contents of rook gizzards to consist of grassland invertebrates. He also found that the food of very young rooks was predominantly of this type (Lockie 1959). Fog (1963) noted that of the eight most frequently represented genera of beetles in rook gizzards, most were likely to have been taken in grassland, albeit from cow dung. These genera belonged to one family, namely Silphidae (carrion beetles). Holyoak (1972) recorded Silphidae from a smaller percentage of rook gizzards, and only then in some months. However, the other animal food most commonly ingested by his specimens, mainly other beetles, tipulids and lepidopterans, were probably taken in grass fields. In fact "grassland insects" featured as common food items in Holyoak's (1968) other study of rook diet. Worthy of note is the fact that Holyoak's

(1972) gizzards were those of birds killed during the Ministry of Agriculture investigation, the report of which (Fisher 1948) revealed most rook flocks to be recorded on grassland. In Holland, Feijen's (1976) analyses conform to the pattern of grassland dwelling invertebrates being amongst the most important animal food items for rooks. The most common food required by New Zealand rooks was reckoned by Purchas (1980) to be that to be found in grass fields. Again in New Zealand, Porter (1979) concluded that the general nature of the rook's food intake was essentially the same as that in Britain, with only different species of grassland invertebrate being taken. So the bulk of the rook's animal diet (which has been recorded to be as high as 56% of the total volume of gizzard contents, Porter 1979) results from feeding on grass fields.

When they were available stubble fields were also heavily utilised by feeding rooks, in some months moreso than grass fields. In all but three months of the study the average flock size of rooks feeding on stubble was also greater than that recorded on grass. As the majority of food items taken in stubble fields is dislodged barley grain (Feare et al 1974), it is clear that during and after harvesting this is an abundant, and therefore presumably important, food source for rooks. Typically, as soon as they became available in August rooks began to feed on harvested barley fields with numbers gradually tailing off as the quality and/or quantity of the food became less good. This could result either from the depredations of the rooks themselves (and other species), or with the ploughing of the fields or with the spreading of dung on them. In the winter of 1978/79 the spreading of dung on stubble was carried out in January whereas in the previous year it was spread in February. A comparison between February 1978 and the same month in 1979 reveals that in the latter year rooks continued to use to a large extent stubble fields

which had been covered with dung but not so large as the use they made of the uncovered stubble fields in 1978. This was despite a greater availability of dung stubble in early 1978 than 1979, and coincided with a partial switch back to grass in the winter of 1979.

The change from other field types to stubble fields is the usual pattern to be noted in studies of rook ecology. For example, in the Aberdeenshire investigation Feare et al (1974) recorded it, as did Feare (1978) in Hampshire and Purchas (1980) in New Zealand, although it was not as marked in the latter case. In Poland, Pinowski (1959) placed little stress on grain in stubble fields as an important food of rooks. Although there was a change to feeding on stubble fields after the harvest the birds seemed to be taking invertebrates in them and switched to mown meadows as soon as they became available. Stubble fields were ploughed more quickly in Pinowski's study area than in the other studies hitherto referred to (including the present one), which could account for there being no prolonged period of feeding in stubble fields in that part of Poland. The overall concentration of feeding rooks in Pinowski's (1959) study seemed to be encountered in parts of the habitat which provided invertebrate food. In both the Hampshire (Feare 1978) and Polish (Pinowski 1959) reports the extent of utilisation of stubble fields was less than that in Aberdeenshire (Feare 1974) and in Fife (this study). The difference between the present investigation and those in Hampshire and Poland could be that no autumn sown cereal fields were available in Fife whereas they were in the other two locations, and in fact were even preferred to stubble in these areas. Autumn sown cereal was available in Aberdeenshire also but the birds did not feed on it to a great degree (Feare 1974), perhaps because it was not very abundant, certainly not as abundant as it was in Hampshire (Feare 1978). Porter (1979), in New Zealand, noted that cereal

figured in rook diet mainly because other food sources were scarce. So the recorded high numbers of rooks feeding in stubble fields, on dislodged grain, is generally accounted for by there being no other preferred food sources available. In this study this was almost certainly the case probably due to reduced numbers of invertebrate prey available in grass fields and the absence of autumn sown cereal.

Analyses of gizzards when stubble fields are available have shown grain to be a common component of rook diet in Britain (Holyoak 1968, 1972) and in Holland (Feijen 1976). There seemed to be little seasonal variation, however, in the amount of grain ingested by Gromadska´s (1980) rooks in Poland. Fog´s (1963) specimens were taken only in spring and early summer, and while cereal grains were a constituent of her gizzards few, if any, were likely to have been taken in stubble fields (see also chapter 6).

As mentioned, in winter 1978/79 covering stubble with dung was done earlier than in the previous year and rooks continued to use this field type in large numbers. Dung stubble was not as heavily used as it was in the previous year. Dung, in the present context, refers to used straw which had been used as indoor bedding for cattle over the winter. The nature of the food which becomes available to rooks when a stubble field is covered with dung will be slightly different from that when the stubble is not covered. Invertebrates will be present to some extent as will cereal grain, in this case barley. The barley will have either remained attached to the straw or passed through the cattle undigested. Dung heaps, which were not used by rooks within the transect area but were by carrion crows (see below), are merely mounds of this material. Dung was never spread on field types other than barley stubble within the transect area. Covering stubble fields with dung was not likely to have been the main reason why rooks resumed using such fields in the winter of

1979, because in the previous year stubble fields which were not spread with dung were also re-used in January and February by a large proportion of rooks. In fact, in February and March 1978 both stubble and dung stubble were available, but most birds were recorded on stubble, notwithstanding its greater availability. Also, despite a greater availability of dung stubble in winter 1978 over winter 1979 a greater proportion of feeding birds were observed on this field type during the latter time. This was so most likely because stubble had ceased to be available and in spite of a greater availability of ploughed fields on which to forage. It seems to be the case, then, that stubble fields are preferred to dung stubble ones. A more detailed discussion of crop availability and rook utilisation appears in the following chapter.

Most stubble fields in the transect area were not spread with dung in late winter but instead were ploughed in late autumn or early winter. The peak time of use of ploughed fields by rooks was during and soon after ploughing (c. 30% of feeding birds), with numbers gradually becoming less (in 1978) with reduced availability of ploughed fields and with the approach of the breeding season. During the breeding season ploughed fields were used to a lesser extent than grass or sown barley fields in Fife. This is in contrast to the situations reported from Hampshire (Feare 1978) and, especially, Aberdeenshire (Feare et al 1974), where ploughed fields were extensively utilised in the breeding season. The reason for the differential use of ploughed fields in the breeding season in Hampshire and Aberdeenshire was judged by Feare (1978) to be because cereal sowing had been completed before the breeding season began in Hampshire, thereby reducing the availability of ploughed or harrowed fields much earlier. In Aberdeenshire barley was sown up to early May in 1971 and oats up to late April, with the availability of all

spring sown cereal fields reaching a peak in the last week of April (Feare 1974). In Fife in 1978 all cereal (barley) sowing had been completed by mid-April and so the number of ploughed fields available to the birds was reduced much earlier there than in Aberdeenshire, which explains the earlier sharp reduction in rook utilisation of this field type in Fife. The dates of cereal sowing depend on the weather and therefore vary from year to year. It is safe to assume, then, that the relative use rooks make of sown cereal and ploughed fields will be governed by sowing dates and, hence, the weather also. This accounts for the more prolonged use of ploughed fields in Aberdeenshire in 1971 (and also in 1966 - Dunnet & Patterson 1968) over Hampshire, and also the observed differences between Aberdeenshire and Fife in the respective years considered. In May in Hampshire fields are prepared for the sowing of maize, and as this also is heavily used by rooks (Feare 1978) it contributes to the extent of the differential use of ploughed fields between Hampshire and Fife. When ploughed fields become available again in autumn and winter rooks resume foraging on them to a high degree (all studies).

As with the Aberdeenshire and Hampshire investigations when sown grain fields were available in Fife they were foraged on by many rooks, and, in fact, they constituted the most important foraging station for rooks in the breeding season. When the barley had germinated (i.e. had become braird) the fields were also utilised but not to the same extent as sown barley or grass fields (in May). Most of the food taken by rooks in sown barley fields is grain (Feare 1974), and it is likely that in braird fields invertebrates were the main food items. Presumably the germinated plants would require too much handling to be efficiently exploited and were never seen to be taken by rooks.

Potato fields were rarely used by rooks in the study area.

In fact, the only time they foraged on this field type was early in the plants' development (May, June) and when they had been lifted (September, October). In between these times the foliage of the plants was too extensive either for the birds to walk freely amongst them or for them to be observed. The former is probably the case given Feare's (1974) observation that the outermost rows of potatoes in a field are the most likely to be attacked by rooks, but this could also mean that birds were still missed during transect counts in this study. Large numbers are probably not involved here though as the observations only refer to one field at any one time. When the shaws of the potatoes were trimmed off and the plants allowed to remain in the soil in order for the tubers to swell further (September) rooks resumed foraging on potatoes but again only a small proportion of all foraging birds at this time did so. When the potatoes had been lifted still only small numbers of rooks used the field. The reason for this limited use of potatoes appears to be that at the time they were available (May, June, September and October) other foraging stations were also available, and to a greater extent, and preferred to potatoes. A similar pattern of use of potatoes was found in Aberdeenshire (Feare 1978), but involved greater numbers of birds.

Rooks scavenged more or less throughout the duration of the study, as evidenced by the (small) numbers of them foraging on waste ground, e.g. roads, gravel paths, etc. The foods available to them here were food thrown away by humans and the occasional rabbit carcass, but they almost certainly captured invertebrate items as well on this "field" type. Scavenging reached a peak in July 1978 on one grass field which had accommodated the Open Golf Championship tented village, though this was recorded under the observations for grass fields.

The only other two field types foraged on by rooks to a notable degree were fallow and sown grass, the same field in fact. As this field lay fallow in September and October 1977 rooks presumably took invertebrates from it. Whatever food items they took, however, must have been present in low densities as the number of rooks observed on it was small. When the field was sown with grass seeds it became immediately more attractive to the birds and was briefly used by greater numbers (only one flock of 80 birds observed). It seems that the birds in this case must have been feeding on the grass seeds though, of course, they could have been taking invertebrates made available by the (mechanical) sowing process.

Of the remaining two foraging stations used by rooks in the study neither were foraged on to any but the slightest degree. The observation of the rook apparently swallowing an item while perched on the back of a sheep is precedented (Editors, British Birds 1944). It is possible that the item ingested was captured before the bird landed on the sheep. Stacks, which more exactly should be called straw bales as the grain had been harvested from them, were also unimportant. Modern farming practices mean that real cereal stacks never appear in the fields, or at least did not in this part of Fife during the study. So a foraging station quite important (though not preferred to grass, for example) in other areas (for instance Aberdeenshire, Feare et al 1974) and before such intensive farming methods became more or less widespread was not available for rooks to exploit.

Effects of snow cover on activity of rooks

In three months, January and February 1978 and January 1979, snow covered the ground of the whole transect area for much of the time. In order to test whether this had an effect on the activity of rooks I examined the distribution of birds seen feeding and not feeding when there was and was not snow on the ground. Table 4.17a (p. 181) shows the results of these tests. Only in January 1979 did the observed distribution suggest that relatively more birds did not feed when there was snow cover. Feare et al (1974) also found lesser proportions of rooks feeding when there was snow present in Aberdeenshire. Clearly, birds here had difficulty finding food on the ground. I also compared the distribution of rooks which were seen flying and those which were "inactive", that is those either resting or in a rookery (Table 4.17b, p. 181). In both January and February 1978 this showed that relatively more birds were observed flying as opposed to being inactive when there was snow cover. These were the times also when no significant differences dependent on snow cover were found between the relative numbers feeding and not feeding. So rooks which were not feeding when there was snow present preferred not to remain inactive either in rookeries or in fields, but to fly. They would probably have been flying in order to find suitable patches of ground on which to forage, but as the earlier result indicates they seem not to have been too successful at this. This is corroborated by the finding that when there were relatively more birds feeding during periods of no snow cover (January 1979) there was no difference between the relative numbers which were flying and those which were inactive with respect to the presence or absence of snow. It seems that when there is no snow rooks do not need to fly around so much looking for feeding sites.

No significant differences regarding snow cover were found with respect to the proportions of rooks engaged in the different non-feeding activities in January 1979. In January 1978, however, a significantly greater proportion was recorded flying over fields than either that resting in a rookery or resting in fields (Table 4.18, p. 182). In the following month a significantly greater proportion was observed resting away from as opposed to in a rookery or flying when there was snow on the ground, and again more rooks were observed flying than perched in a rookery. So at the times when snow cover led to a significantly greater proportion of birds to be recorded flying rather than being inactive those which in fact were observed resting preferred to do so away from a rookery. When there is a layer of snow present then rooks presumably do not sit in rookeries because it is too cold. In rookeries they will be more exposed to wind, and the resulting heat loss will be exarcebated by sitting on snow covered branches. Heat loss through the feet may also be a problem on or near the ground but at least there will be a greater chance of obtaining shelter there.

In order to test whether snow cover had an effect on the field types which rooks foraged on I compared the total numbers of birds seen within the same month on various field types with and without snow cover. Table 4.19 (p. 183) shows the results of those tests which could be carried out. Rooks seemed to prefer stubble when there was snow on the ground, but used it proportionately less than grass or ploughed fields when there was no snow. This applied to dung covered stubble as well. There was no tendency to forage on grass rather than ploughed fields or vice versa when there was snow cover. Feare et al (1974) also noted a greater (though not significantly so) use of stubble than grass during periods of snow cover, but dung and stacks were the only foraging stations used for

more than 20% of the total foraging time. Stacks were not available in this study (see above) but the observation regarding dung in January 1979 confirms the Aberdeenshire finding. In Aberdeenshire the amount of food obtained by rooks from various foraging stations was reflected in the times spent on those foraging stations, so presumably the same is true in Fife. The reason why proportionately more rooks forage on stubble when there is snow cover is probably because grain is easier to locate on stubble fields than the food available on grass or ploughed fields is. The nature of stubble is such that a greater surface area of plant material is exposed on a field containing it than is on a grass field. The cut stems of the barley plants are hard and often very close together as well as being up to 15 cm high, sometimes more. They thus can trap snow and prevent as much of it from reaching the ground, and may also shelter other parts of the ground from snow as well. Therefore, snow cover on a stubble field will be thinner than on a short grass or ploughed field. Stubble fields, indeed, look as though there is not as much snow on them as neighbouring grass fields. If the snow fall has not been very heavy any food items on a stubble field will probably be even more accessible to rooks than those on a grass field.

Patterson (1975) found that rooks in snow covered fields tended to show high rates of aggression towards one another, probably as a result of reduced spacing between them. In Fife also, where rooks on stubble tended to congregate on patches of the fields where snow cover was thinnest, I observed them to be closer together and to squabble frequently. Patterson (1975) noted that spacing between individual rooks was less on "grain crops" than on grass.

Carrion crow numbers

The number of carrion crows on each transect count remained fairly constant at about two throughout the study. The transect area included, however, parts of the territories of four pairs of crows. Three of these pairs were not as frequently observed as one pair. In addition to these territory holding crows a flock (of presumably non territorial birds) inhabited parts of the west end of the area near the River Eden estuary in autumn 1977 to spring 1978. The peak size of this flock was 21 birds in October 1977 but only about half of these remained by May 1978. In the following September a flock of 25 crows was observed on the Eden estuary bed, but it is not clear where these birds came from, nor whether they included birds which had been members of the flock in the previous year. It is likely that these flocks were comprised of first year birds (Wittenberg 1968, Charles 1972), so perhaps crows from a wider area than that sampled here comprised them. Adults may also join flocks. Loman (1980a) noted that Swedish hooded crow flocks increased the size of their home range after April which, if the same is true for carrion crow flocks, could explain the "disappearance" of the Eden estuary flock from the study area at this time. As with rooks, carrion crows from the continent do not appear to migrate to Scotland, and the resident population is relatively sedentary (Busse 1969, Holyoak 1971). The fact that no significant seasonal differences were found in the number of crows observed throughout this study confirms this.

General activity of carrion crows

As with rooks the predominant activity of carrion crows observed on the transect counts was feeding. Greater proportions of

resting crows were recorded in late autumn/early winter. The proportions of crows seen which were flying remained fairly, but not entirely, constant throughout at around 15-20% (see Fig. 4.24, p. 206).

All carrion crows observed in March 1978 were feeding. The exact locations of the nests of three of the four pairs inhabiting the transect area were not ascertained. The fourth was built in a Scots pine tree (as the others could have been) and so observing birds at the nest while on the transect was difficult. This accounts in part for the fact that no birds were observed other than those feeding in fields at this time of year when (in mid to late March) carrion crows in N.E. Fife as a whole were nest-building. Rather puzzling is that no crows were seen flying over fields in this month either, though they would not necessarily have been spotted flying to collect nest material. Few crows were seen resting at this time of year also (none at all in March), again reflecting the priority breeding activities take. The proportion of birds resting reached a peak in the summer, though the proportions feeding remained somewhat stable during this period despite the birds being in moult then. The reason that crows were able to spend more of their time resting in summer is likely to be simply that the pressures of breeding activity (in its widest sense) were relaxed. At times other than in the breeding season feeding and feeding related behaviours are the most important ones for the survival of carrion crows. The proportion of carrion crows seen feeding throughout the study was variable but not extremely so (s.d. = 17.85%, range = 40-100%). Outside the breeding season the greatest proportions of feeding crows were observed in September 1978 and January and February 1979, times which also coincided with low proportions of resting birds. Similarly, higher proportions of resting crows coincided with lower proportions of

feeding ones (for example November and December 1978). The proportions of crows seen flying in throughout the study were, unlike rooks, constant (s.d. = 9.41%, range = 0-33.33%).

Crows are territorial for the whole year. Therefore, they will get to know the physical and ecological characteristics of their territory very well, and it is likely that their food supply is of a more predictable nature than that of rooks. Rooks range over greater distances throughout the year, especially in winter (see above), and also their food supply is more unpredictable, so therefore they are probably less familiar with the nature of the area they inhabit than crows are. For these reasons, then, flying in the two species is likely to be somewhat different from a motivational point of view. Specifically, crows fly to patrol their territory and also to particular locations within it usually to search for food, whereas rooks are more likely to search for conspecific flocks, which, in a sense, is already part of the food finding process. Thus, any relationship between feeding and flying is less obvious in crows than in rooks as crows do not feed socially to the extent that rooks do. This, perhaps indirectly, accounts for the relationship between resting and feeding in crows. When feeding is not a priority activity crows can devote more time to resting while maintaining normal levels of flying.

Feeding certainly was a priority activity in March 1978 and also in February 1979 when over 90% of crows seen were foraging. This could be because they required more food in preparation for breeding. As stated, the proportions seen feeding in other months were variable within limits, and there appeared to be a trend (non-significant) towards a cyclical fluctuation generally over time with lower proportions recorded in summer and late autumn/early winter, and higher proportions in spring, late summer and late

winter. If the same argument as was applied earlier to rook foraging patterns is applied to crows also then this could mean that the amount of food available to crows was lower during these latter times than during the former ones. This makes sense in the light of the probability that the time when young birds are being reared coincides with a peak in food availability. (Lack 1950, 1954). Lockie (1955) showed this to be true for the jackdaw, and also for the rook as far as animal food (especially earthworms) was concerned. The evidence regarding the carrion crow was also suggestive of this but somewhat more circumstantial.

Use of the various feeding stations by carrion crows

An important foraging station of carrion crows was present in the transect area but was not represented in the observations because birds using it were impossible to see. This was woodland, especially the woodland floor, which was used by crows for foraging on when food requirements were high in the breeding season and in cold weather in Oxfordshire (Lockie 1955). The extent to which crows used woodland in the study area of N.E. Fife is not known, so the possibility exists that the recorded pattern of field use by them is somewhat different from their actual relative use of fields. Any difference though will be minor as crows were never seen foraging on the woodland floor in the transect area (or in other parts of Fife) during casual observations or during rook census work. In fact, they might not use this foraging station at all in Fife.

The field type most frequently used by foraging crows was, as with rooks, grass. It is not known from which kinds of fields crows obtain the bulk of the invertebrate part of their food intake, but the few recent studies of crow diet suggest that grass fields are

important (Lockie 1955, 1956b, Holyoak 1968), though woodland cannot be ruled out here as a significant foraging station. Earthworms constituted part of the diet of carrion crows at all times of the year in Lockie's (1956b) study. While most of these were taken in grassland, an unknown proportion might have been taken in woodlands. Of the other significant items of animal food in the diet of crows, viz. carrion, small mammals and nestling birds (Lockie 1955, Holyoak 1968), the latter would not be found in grassland to the same extent as the other two. Again, all three food types could be taken in woodland (but perhaps in other foraging sites as well), especially mammals and birds. Carrion would probably be very likely to be eaten in grass fields if only by virtue of the abundance of this field type. Waste ground (and especially roads) is another likely place where carrion may be exploited by crows. Roads were generally used more often by crows than by rooks in the study, particularly in the summer. This is the time also when most bird mortality takes place on roads (Dunthorn & Errington 1964).

The second most important field types used by carrion crows were, collectively, barley fields. These included stubble fields which were heavily utilised when available, sown barley and braird fields. The monthly pattern here conforms closely with the monthly incidence of grain found in the gizzards of Lockie's (1956b) specimens, though Holyoak (1968) reported high percentages of his gizzards to contain grain in all months of the year. The availability of grain fields of one sort or another in either of these studies was not reported. It is likely, however, that if crow gizzards had been analysed in this study then grain would have been recorded throughout the year as it was always available, albeit to varying extents. Another important foraging station for crows was dung, being either dung covered stubble or dung heaps, from both of

which grain could have been taken, but especially from the former. Crows used sown barley and braird fields to about the same extent as rooks but they foraged on stubble much less than rooks. Rowley (1973) coined the term 'swamping' whereby flocks of birds were able to feed unmolested in the territories of territorial species. He noted this intraspecifically and also interspecifically in Australian corvids, flocks of the little raven C. mellori swamping the larger, territorial Australian raven C. coronoides. Though there is no direct evidence for swamping of crows by rooks in the present study there is a suggestion perhaps that crows were avoiding large rook flocks. When stubble was available the largest feeding rook flock sizes on any field type (other than the one observed flock of 80 rooks on sown grass) were recorded on it. The evidence of possible avoidance of rooks by crows comes from the pattern of use of stubble by the two species. For example, when rooks ceased foraging on stubble in December 1978 crows resumed using it. A similar pattern was evident in the use of dung covered stubble by the two species in early 1978, when crows appeared to stop using it when large flocks of rooks began to. There was no obvious suggestion that this was happening on grass fields, perhaps for two important reasons. The first is that grass fields were much more abundant than other fields, so the data refer to a much larger area. The second is that rook flock sizes were generally much smaller on grass than on stubble fields. Carrion crows used dung heaps in the summer whereas rooks did not do so at all in the transect area. Outside this area rooks did forage on dung heaps, as mentioned earlier, but flock sizes on them were generally smaller than average feeding flock sizes (only in the order of about ten birds), and certainly a lot smaller than the mean size of those recorded on stubble fields. Rooks, therefore, may have been unable to swamp crows on these small, localised food

patches, where intraspecific conflict was high anyway, and also where crows may have been able to drive off such small rook flocks.

The proportions of feeding crows observed doing so on ploughed fields seem high in some months (see Fig. 4.19, p. 202), but the actual numbers (Table 4.11, p. 174) were low. It is also clear here that crows were outnumbered by rooks using the same ploughed fields. Again the possibility exists that crows were being swamped by rooks, leading to an avoidance by crows of fields on which large numbers of rooks were foraging. The data, however, suggest that ploughed fields were not places on which crows depended to any significant extent for their food requirements, except perhaps in November 1978. The fact that they were never seen foraging in a field when a tractor was in the process of ploughing or cultivating it suggests that they were more wary than rooks of human activity. When a tractor was ploughing many birds of several species, especially rooks, black-headed gulls Larus ridibundus and starlings Sturnus vulgaris, and occasionally lapwings Vanellus vanellus and other gulls Larus spp., followed it. Perhaps crows were again avoiding such large, and in this case mixed species, flocks.

In virtually all months crows were observed foraging on the intertidal mud of the River Eden estuary at Guardbridge. Estuarine or marine food did not figure in the analyses of gizzards made by Lockie (1955, 1956a) or Holyoak (1968). The reasons for this are that the former studies were conducted in Oxfordshire which is landlocked, and Holyoak's gizzards were from birds taken in farmland areas, though some of these must have been coastal. Most of the fish carrion recorded by Holyoak (1968) was probably scavenged from human rubbish sites. The food exploited by crows in the River Eden mud is not known but it was likely to have been small invertebrates. Crows were never seen handling any large shellfish here for example. They

always fed on the river bed itself and were not seen carrying prey to the banks of the river. Nor were they seen dropping shellfish to crack them open. They sometimes foraged on the rocks in St. Andrews Bay, where they competed actively with gulls for food items.

The sown grass field available in June 1978 figured as a fairly important foraging site for crows. As with rooks, they could either have been taking grass seeds or invertebrates here. With young to feed and the summer moult under way, however, the latter is more likely. The same probably applies to their use of sown potato fields at this time also. If crows were feeding on potatoes in September 1978 then the low frequency of occurrence on this field type (only two birds) is in keeping with the low proportions of gizzards containing potato fragments in Holyoak's (1968) study. The same is true with regard to fodder for farm animals. Holyoak (1968) reported only 2% of his gizzards to contain it and only one crow in the present study was observed feeding at a cow trough. Feeding troughs were rarely available in the transect area. The only other foraging station which crows used in this study was trees. Two crows in May 1978 and one in the following month were observed ingesting food while perched in trees but it was not identified. It need not have been food which had been captured in trees, of course.

Table 4.1. The number of transects made at different times of the day in each month of the habitat use study. "Morning" denotes transects made up to 1200hrs, "early afternoon" is 1200-1500hrs, "late afternoon" 1500-1800hrs and "evening" means transects started after 1800hrs G.M.T.

	Morning	Early Afternoon	Late Afternoon	Evening	Total
September 1977	11	7	1	7	26
October 1977	16	6	9	3	34
November 1977	2	3	0	0	5
December 1977	10	0	0	0	10
January 1978	16	7	1	0	24
February 1978	11	10	6	0	27
March 1978	19	2	14	4	39
April 1978	10	3	11	2	26
May 1978	18	4	16	5	43
June 1978	17	2	12	3	34
July 1978	13	1	11	6	31
August 1978	17	1	11	4	33
September 1978	15	4	9	3	31
October 1978	12	2	4	1	19
November 1978	12	2	4	0	18
December 1978	6	1	0	0	7
January 1979	6	3	4	0	13
February 1979	5	1	1	0	7
Total	216	59	114	38	427

Table 4.2. Total numbers of rooks seen at different times of the day in each month of the study. Those numbers marked with an asterisk (*) are possible underestimates due to the difficulty in accurately estimating the numbers of birds in rookeries.

	Morning	Early Afternoon	Late Afternoon	Evening	Total
September 1977	821*	995	13	1602*	3431*
October 1977	1460*	643	1356	457	3916*
November 1977	44	295	106	0	445
December 1977	388*	0	0	0	388*
January 1978	578	357	11	0	946
February 1978	431	278	335	0	1044
March 1978	778*	36*	764*	168*	1746*
April 1978	174*	123*	251*	77*	625*
May 1978	472*	296*	594*	151*	1513*
June 1978	498	107	722	49	1376*
July 1978	308	20	411	117	856
August 1978	358*	49	273	99	779*
September 1978	730	9	708	302	1749
October 1978	915	302	669	189	2075
November 1978	841*	153	58*	0	1052*
December 1978	552*	305	0	0	857*
January 1979	320*	138	102	0	560*
February 1979	851	101	19	0	971
Total	10519	4207	6392	3211	24329

Table 4.3. Total numbers of carrion crows seen at different times of the day in each month of the study.

	Morning	Early Afternoon	Late Afternoon	Evening	Total
September 1977	-	-	-	-	-
October 1977	42	0	49	0	91
November 1977	-	-	-	-	-
December 1977	-	-	-	-	-
January 1978	-	-	-	-	-
February 1978	-	-	-	-	-
March 1978	13	21	19	0	53
April 1978	17	3	70	15	105
May 1978	26	22	55	15	118
June 1978	28	3	37	9	77
July 1978	21	4	26	18	69
August 1978	28	6	37	13	84
September 1978	59	9	7	5	80
October 1978	31	2	9	0	42
November 1978	32	8	16	0	56
December 1978	15	0	0	0	15
January 1979	20	4	0	0	24
February 1979	30	1	0	0	31
Total	362	83	325	75	845

Table 4.4. Total numbers of rooks seen feeding at different times of the day in each month of the study.

	Morning	Early Afternoon	Late Afternoon	Evening	Total
September 1977	687	760	1	1074	2522
October 1977	1002	539	626	56	2223
November 1977	0	207	80	0	287
December 1977	185	0	0	0	185
January 1978	200	264	0	0	464
February 1978	231	206	67	0	504
March 1978	164	2	186	4	356
April 1978	143	94	118	1	356
May 1978	307	259	354	78	998
June 1978	418	101	549	39	1107
July 1978	289	17	372	95	773
August 1978	321	47	236	75	679
September 1978	349	4	427	76	856
October 1978	616	236	358	30	1240
November 1978	425	61	0	0	486
December 1978	308	147	0	0	455
January 1979	226	112	30	0	368
February 1979	714	25	12	0	751
Total	6585	3081	3416	1528	14610

Table 4.5. Total numbers of carrion crows seen feeding at different times of the day in each month of the study.

	Morning	Early Afternoon	Late Afternoon	Evening	Total
September 1977	-	-	-	-	-
October 1977	42	0	45	0	87
November 1977	-	-	-	-	-
December 1977	-	-	-	-	-
January 1978	-	-	-	-	-
February 1978	-	-	-	-	-
March 1978	13	21	19	0	53
April 1978	10	0	63	15	88
May 1978	13	16	42	2	73
June 1978	14	3	28	9	54
July 1978	11	2	18	12	43
August 1978	16	5	28	9	58
September 1978	49	7	7	5	68
October 1978	23	0	6	0	29
November 1978	19	6	4	0	29
December 1978	6	0	0	0	6
January 1979	18	2	0	0	20
February 1979	29	0	0	0	29
Total	263	62	260	52	637

Table 4.6. Mean flock sizes of feeding rooks on all field types combined for every month of the study and at each time of the day. The number of observations (i.e. number of flocks) is given in brackets.

	Morning	Early Afternoon	Late Afternoon	Evening	Overall means
September 1977	21.47 (32)	33.04 (23)	1.00 (1)	76.71 (14)	36.03 (70)
October 1977	14.11 (71)	21.56 (25)	20.87 (30)	28.00 (2)	17.37 (128)
November 1977	- (-)	18.82 (11)	80.00 (1)	- (-)	23.92 (12)
December 1977	10.28 (18)	- (-)	- (-)	- (-)	10.28 (18)
January 1978	16.67 (12)	17.6 (15)	- (-)	- (-)	17.19 (27)
February 1978	12.83 (18)	29.43 (7)	7.44 (9)	- (-)	14.82 (34)
March 1978	5.13 (32)	2.00 (1)	5.81 (32)	4.00 (1)	5.39 (66)
April 1978	8.41 (17)	23.5 (4)	6.56 (18)	1.00 (1)	8.90 (40)
May 1978	11.81 (26)	16.19 (16)	7.7 (46)	5.57 (14)	9.78 (102)
June 1978	14.93 (28)	25.25 (4)	14.84 (37)	7.8 (5)	14.96 (74)
July 1978	11.12 (26)	8.50 (2)	13.29 (28)	5.94 (16)	10.74 (72)
August 1978	12.35 (26)	11.50 (4)	7.61 (31)	37.75 (2)	10.78 (63)

Table 4.6 (continued)

September 1978	11.26 (31)	1.33 (3)	20.33 (21)	38.00 (2)	15.02 (57)
October 1978	14.67 (42)	29.50 (8)	35.80 (10)	30.00 (1)	20.33 (61)
November 1978	18.48 (23)	20.33 (3)	- (-)	- (-)	18.69 (26)
December 1978	34.22 (9)	49.00 (3)	- (-)	- (-)	37.92 (12)
January 1979	25.11 (9)	22.40 (5)	30.00 (1)	- (-)	24.53 (15)
February 1979	44.63 (16)	6.25 (4)	6.00 (2)	- (-)	34.14 (22)
Overall means	15.10 (436)	22.33 (138)	12.79 (267)	26.34 (58)	16.25 (899)

Table 4.7. The overall mean flock sizes of rooks feeding on grass at different times of the day and in the different months of the study. The number of observations (i.e. the number of flocks) is given in brackets after each mean flock size.

September 1977	36.39	(36)			
October 1977	15.83	(78)			
November 1977	15.25	(8)			
December 1977	10.80	(10)			
January 1978	14.33	(12)			
February 1978	3.81	(16)	Mornings	14.59	(281)
March 1978	3.85	(34)	Early Afternoons	19.22	(76)
April 1978	6.82	(11)	Late Afternoons	11.83	(163)
May 1978	10.77	(60)	Evenings	23.97	(37)
June 1978	16.89	(63)			
July 1978	11.01	(70)			
August 1978	11.00	(53)	Overall	15.04	(557)
September 1978	9.33	(24)			
October 1978	12.68	(34)			
November 1978	21.26	(19)			
December 1978	36.88	(8)			
January 1979	22.38	(8)			
February 1979	43.46	(13)			

Table 4.8. The overall mean flock sizes of rooks feeding on stubble at different times of the day and in the different months of the study when it was available. The number of observations (i.e. the number of flocks) is given in brackets after each mean flock size.

September 1977	43.52	(25)			
October 1977	27.25	(28)			
November 1977	20.00	(2)			
December 1977	5.00	(1)			
January 1978	43.80	(5)			
February 1978	40.56	(9)	Mornings	26.44	(62)
March 1978	3.50	(2)	Early Afternoons	34.28	(29)
August 1978	63.00	(1)	Late Afternoons	37.59	(22)
September 1978	23.38	(26)	Evenings	57.78	(9)
October 1978	40.21	(19)			
November 1978	11.00	(4)	Overall	32.62	(122)

Table 4.9. The total numbers of rooks and carrion crows observed feeding or foraging on various field types/foraging stations. Data are for 18 months for rooks and 13 months for crows.

	No. of rooks	No. of crows
GRASS	8376	285
PLOUGH	728	22
STUBBLE	3980	79
MUDFLATS	0	40
WASTE	118	23
SOWN BARLEY	579	84
BRAIRD	117	22
DUNG	385	65
POTATOES	69	2
PLOUGHING IN PROGRESS	124	0
SOWN POTATOES	21	4
FALLOW	25	0
TREES	0	3
SOWN GRASS	80	7
STACKS	7	0
ANIMAL TROUGHS	0	1
SHEEP'S BACK	1	0
TOTAL	14610	637

Table 4.10. The numbers of rooks and carrion crows observed foraging on grass, stubble and sown barley in each month of the study.

	GRASS		STUBBLE		SOWN BARLEY	
	Rooks	Crows	Rooks	Crows	Rooks	Crows
September 1977	1310	-	1102	-	-	-
October 1977	1235	11	763	72	-	-
November 1977	122	-	40	-	-	-
December 1977	108	-	5	-	-	-
January 1978	172	-	219	-	-	-
February 1978	61	-	365	-	-	-
March 1978	131	7	7	-	209	21
April 1978	75	24	-	-	212	63
May 1978	646	42	-	-	158	-
June 1978	1064	28	-	-	-	-
July 1978	771	32	-	-	-	-
August 1978	583	52	63	-	-	-
September 1978	224	32	608	3	-	-
October 1978	431	17	764	2	-	-
November 1978	404	20	44	-	-	-
December 1978	295	2	-	2	-	-
January 1979	179	11	-	-	-	-
February 1979	565	7	-	-	-	-
Total	8376	285	3980	79	579	84

Table 4.11. The numbers of rooks and carrion crows observed foraging on braird, plough and land in the process of being ploughed in each month of the study.

	BRAIRD		PLOUGH		CULT. IN PROGRESS	
	Rooks	Crows	Rooks	Crows	Rooks	Crows
September 1977	-	-	86	-	-	-
October 1977	-	-	210	4	-	-
November 1977	-	-	45	-	-	-
December 1977	-	-	52	-	-	-
January 1978	-	-	55	-	-	-
February 1978	-	-	41	-	-	-
March 1978	-	-	-	-	-	-
April 1978	-	-	-	-	59	-
May 1978	116	22	-	4	53	-
June 1978	1	-	-	-	-	-
July 1978	-	-	-	2	-	-
August 1978	-	-	10	-	-	-
September 1978	-	-	2	-	-	-
October 1978	-	-	-	-	5	-
November 1978	-	-	38	6	-	-
December 1978	-	-	153	1	7	-
January 1979	-	-	1	1	-	-
February 1979	-	-	35	4	-	-
Total	117	22	728	22	124	-

Table 4.12. The numbers of rooks and carrion crows observed foraging on dung (heaps and dung covered stubble), waste and potatoes in each month of the study.

	DUNG		WASTE		POTATOES	
	Rooks	Crows	Rooks	Crows	Rooks	Crows
September 1977	-	-	2	-	-	-
October 1977	-	-	6	-	-	-
November 1977	-	-	-	-	-	-
December 1977	-	-	20	-	-	-
January 1978	-	-	18	-	-	-
February 1978	37	-	-	-	-	-
March 1978	9	25	-	-	-	-
April 1978	-	-	10	-	-	-
May 1978	-	-	4	-	-	-
June 1978	-	15	3	-	38	-
July 1978	-	2	1	3	-	-
August 1978	-	1	23	2	-	-
September 1978	-	1	5	5	17	2
October 1978	-	-	26	5	14	-
November 1978	-	-	-	3	-	-
December 1978	-	-	-	-	-	-
January 1979	188	5	-	3	-	-
February 1979	151	4	-	-	-	-
Total	385	53	118	21	69	2

Table 4.13. The numbers of rooks and carrion crows observed foraging on sown potatoes, the Eden mudflats and fallow ground in each month of the study.

	SOWN POTATOES		MUDFLATS		FALLOW	
	Rooks	Crows	Rooks	Crows	Rooks	Crows
September 1977	-	-	-	-	17	-
October 1977	-	-	-	-	8	-
November 1977	-	-	-	-	-	-
December 1977	-	-	-	-	-	-
January 1978	-	-	-	-	-	-
February 1978	-	-	-	-	-	-
March 1978	-	-	-	-	-	-
April 1978	-	-	-	1	-	-
May 1978	21	2	-	1	-	-
June 1978	-	2	-	1	-	-
July 1978	-	-	-	3	-	-
August 1978	-	-	-	1	-	-
September 1978	-	-	-	25	-	-
October 1978	-	-	-	5	-	-
November 1978	-	-	-	-	-	-
December 1978	-	-	-	1	-	-
January 1979	-	-	-	-	-	-
February 1979	-	-	-	2	-	-
Total	21	4	-	40	25	-

Table 4.14. The numbers of rooks and carrion crows seen foraging at stations other than those represented in Tables 4.10 to 4.13. The months of observations are given also.

SOWN GRASS:	80 rooks (November 1977); 7 carrion crows (June 1978)
STACKS:	7 rooks (5, September 1977; 1, June 1978; 1, July 11978)
TREES:	3 carrion crows (2, May 1978; 1, June 1978)
SHEEP'S BACK:	1 rook (October 1977)
COW FEEDING TROUGH:	1 carrion crow (July 1978)

Table 4.15. The proportions of feeding rooks and crows which did so on the same field type in the same month. All comparisons were made on the raw data using the chi square test (see text). The 'Rook' column contains the proportion (expressed as a percentage) of the monthly total of feeding rooks observed feeding on the field type in question, and the 'Crow' column the corresponding proportion of carrion crows. The 'X^2' column gives the chi square value (1 d.f.) associated with the difference in these proportions, and the 'p' column the probability associated with the difference. Significant differences are marked with an asterisk (*). 'n.a.' (not applicable) indicates that rules for chi square are violated.

		Rook	Crow	X^2	p
October 1977:	Grass	55.56	12.64	60.34	$<.001^*$
	Stubble	34.32	82.76	83.01	$<.001^*$
	Plough	9.45	4.60	1.80	$>.05$
March 1978:	Grass	36.80	13.21	10.45	$<.001^*$
	Sown Barley	58.71	39.62	38.56	$<.001^*$
	Dung Stubble	2.53	47.17	114.83	n.a.
April 1978:	Grass	21.07	27.27	1.23	$>.05$
	Sown Barley	59.55	71.59	3.84	$<.05^*$
May 1978:	Grass	64.73	57.53	1.24	$>.05$
	Braird	11.62	30.14	19.16	$<.001^*$
	Sown Potatoes	2.10	2.74	0.003	n.a.
June 1978:	Grass	96.12	51.85	172.64	n.a.
July 1978:	Grass	99.74	74.42	150.85	n.a.
	Waste	0.13	6.98	26.37	n.a.
August 1978:	Grass	85.86	89.66	0.37	$>.05$
	Waste	3.39	6.90	0.12	n.a.
September 1978:	Grass	26.17	47.06	12.70	$<.001^*$
	Stubble	71.03	4.41	121.85	$<.001^*$
	Potatoes	1.96	2.94	0.008	n.a.
	Waste	0.58	7.35	21.01	n.a.

Table 4.15 (continued)

		Rook	Crow	x^2	p
October 1978:	Grass	34.76	58.62	6.06	$<.05^*$
	Stubble	61.61	6.90	33.21	$<.001^*$
	Waste	2.10	17.24	21.29	n.a.
November 1978:	Grass	83.13	68.97	2.86	$>.05$
	Plough	7.82	20.69	4.27	n.a.
December 1978:	Grass	64.84	33.33	1.37	n.a.
	Plough	33.63	16.67	0.19	n.a.
January 1979:	Grass	48.64	55.00	0.11	$>.05$
	Dung Stubble	51.09	25.00	4.17	$<.05^*$
	Plough	0.27	5.00	1.62	n.a.
February 1979:	Grass	75.23	24.14	34.71	$<.001^*$
	Plough	4.66	13.79	3.17	n.a.
	Dung Stubble	20.11	55.17	0.36	$>.001$

Table 4.16. The field types which were used by only one species. The 'Rook' column gives those field types which were used by rooks but not by carrion crows in each month, and the 'Crow' column gives those which were used by carrion crows but not by rooks.

	Rook	Crow
October 1977:	Waste Fallow Sheep's back	None
March 1978:	Stubble	None
April 1978:	Plough in progr. Waste	Mudflats
May 1978:	Plough in progr. Waste Sown Barley	Mudflats Plough Trees
June 1978:	Braird Potatoes Stacks Waste	Mudflats Sown potatoes Sown grass Dung Trees
July 1978:	Stacks	Mudflats Plough Dung Animal trough
August 1978:	Stubble Plough	Mudflats Dung
September 1978:	Plough	Mudflats Dung
October 1978:	Plough in progr. Potatoes	Mudflats
November 1978:	Stubble	Mudflats Waste
December 1978:	Plough in progr.	Stubble Mudflats
January 1979:	None	Waste
February 1979:	None	Mudflats

Table 4.17. (a) The numbers of rooks which were observed feeding and not feeding in the three months of the study when snow cover was recorded. (b) The numbers of rooks which were observed flying and "inactive" (those resting + those in a rookery) when there was and was not snow cover. Tests used were 2x2 chi square. Significant values are denoted by an asterisk (*).

(a)

January 1978	SNOW	NO SNOW	X^2	d.f.	p
No. rooks FEEDING	50	414			
No. rooks NOT FEEDING	39	443	1.70	1	>.05
February 1978					
No. rooks FEEDING	218	286			
No. rooks NOT FEEDING	210	330	1.88	1	>.05
January 1979					
No. rooks FEEDING	195	173			
No. rooks NOT FEEDING	133	59	13.12	1	<.001*

(b)

January 1978	SNOW	NO SNOW	X^2	d.f.	p
No. rooks INACTIVE	11	368			
No. rooks FLYING	28	61	73.26	1	<<.001*
February 1978					
No. rooks INACTIVE	111	242			
No. rooks FLYING	47	55	6.84	1	<.01*
January 1979					
No. rooks INACTIVE	43	24			
No. rooks FLYING	86	33	0.97	1	>.05

Table 4.18. The numbers of non-feeding rooks engaged in various activities when there was and was not snow cover. Only those 2x2 chi square tests which could be made without violating the requirements of the test are reported. Significant chi square values are denoted by an asterisk (*).

January 1978	SNOW	NO SNOW	X^2	d.f.	p
No. rooks RESTING	3	94			
No. rooks FLYING	28	61	24.89	1	<.001*
No. rooks FLYING	28	61			
No. rooks IN ROOKERY	8	274	60.03	1	<<.001*
February 1978					
No. rooks RESTING	53	28			
No. rooks FLYING	47	55	6.07	1	<.02*
No. rooks FLYING	47	55			
No. rooks IN ROOKERY	58	214	21.30	1	<.001*
No. rooks RESTING	53	28			
No. rooks IN ROOKERY	58	214	54.30	1	<<.001*
January 1979					
No. rooks RESTING	8	7			
No. rooks IN ROOKERY	35	17	0.47	1	>.05
No. rooks FLYING	86	33			
No. rooks IN ROOKERY	35	17	0.22	1	>.05

Table 4.19. The numbers of rooks observed foraging on various field types when there was and was not snow cover. The table only includes the data which did not violate the requirements of the 2x2 chi square test. Significant chi square values are denoted by an asterisk (*).

February 1978	SNOW	NO SNOW	x^2	d.f.	p
No. rooks on GRASS	10	51			
No. rooks on STUBBLE	198	167	28.48	1	<.001*
No. rooks on GRASS	10	51			
No. rooks on PLOUGH	10	31	0.55	1	>.05
No. rooks on PLOUGH	10	31			
No. rooks on STUBBLE	198	167	11.98	1	<.001*
January 1979					
No. rooks on GRASS	19	160			
No. on DUNG STUBBLE	175	13	246.98	1	<<.001*

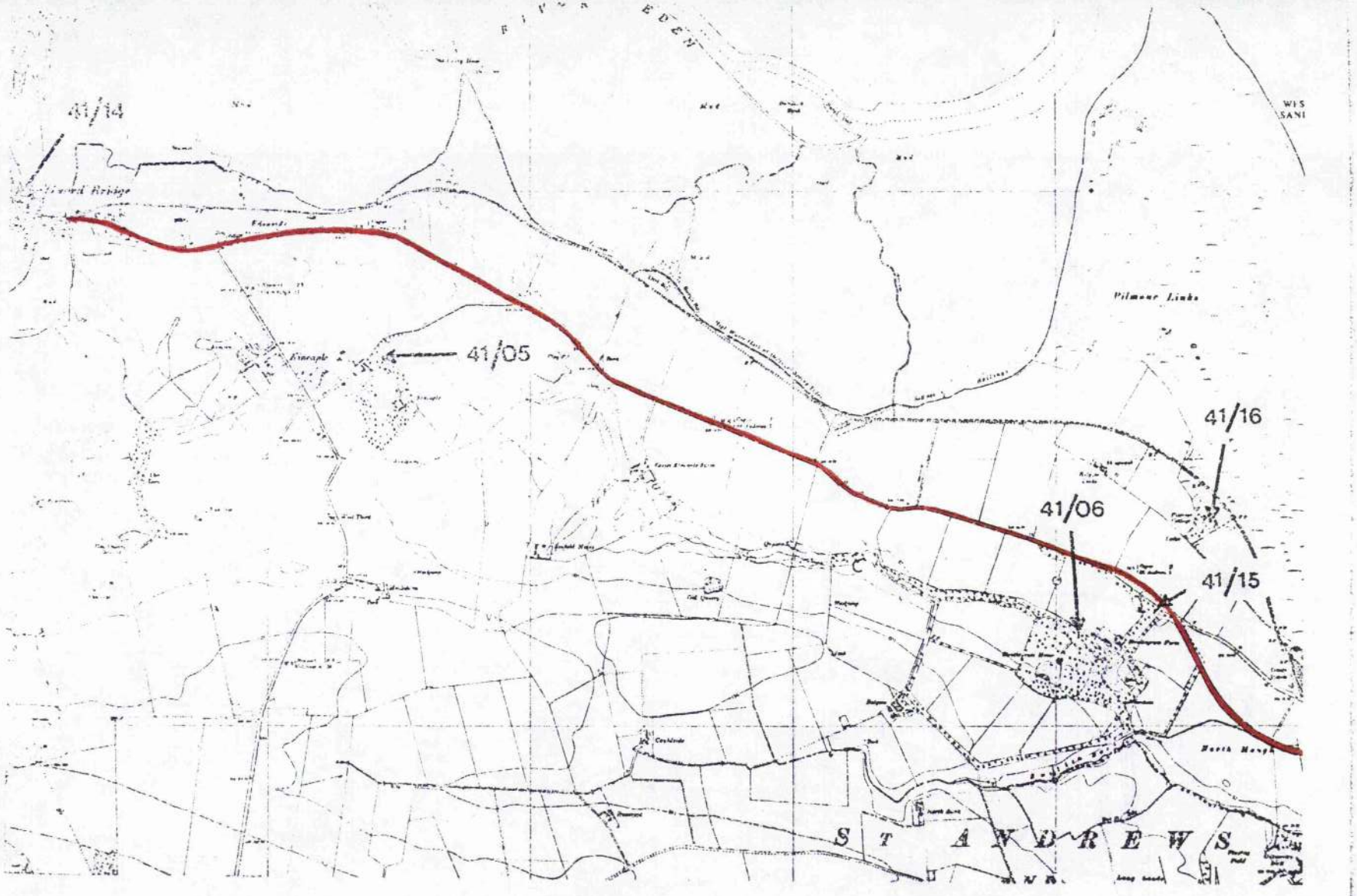


Figure 4.1 Map of the transect area (1:50 000) showing the road along which counts were made, adjoining fields and locations of the five rookeries within the area.

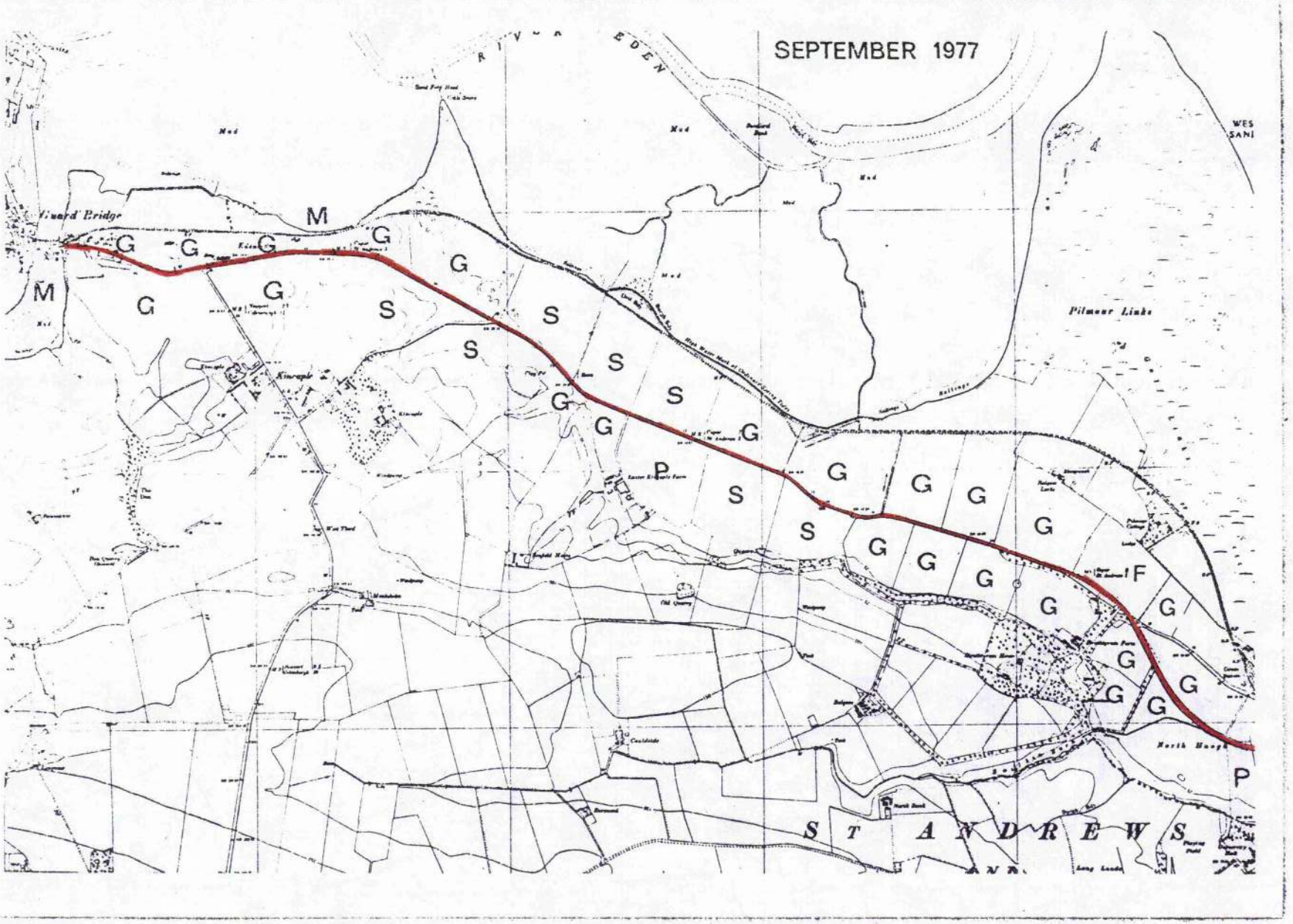


Figure 4.2 Map of the transect area showing field types present in September 1977.
G - grass; S - stubble; P - plough; M - mud; F - fallow.

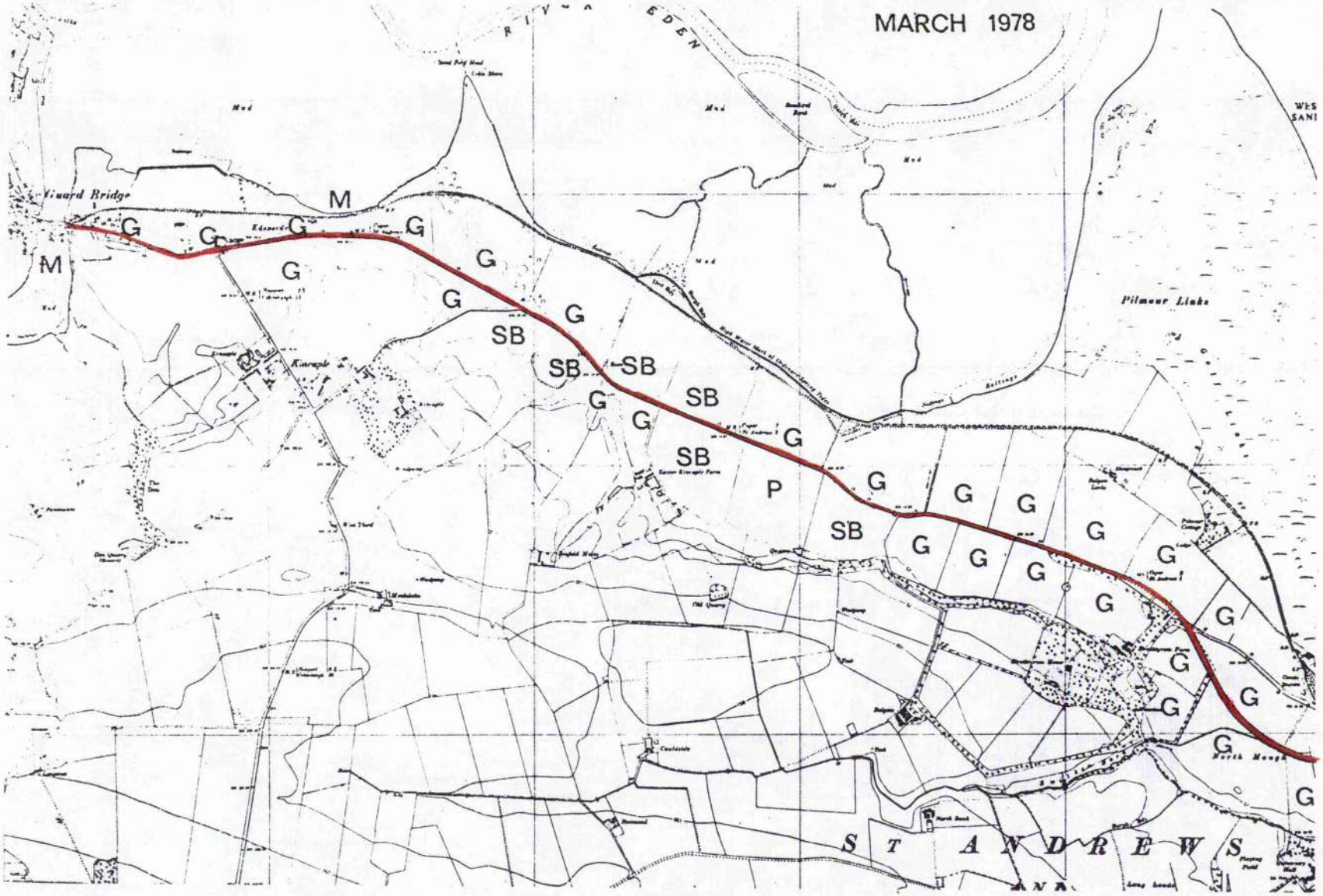


Figure 4.3 Map of the transect area showing field types present in March 1978.
G - grass; P - plough; M - mud; SB - sown barley.

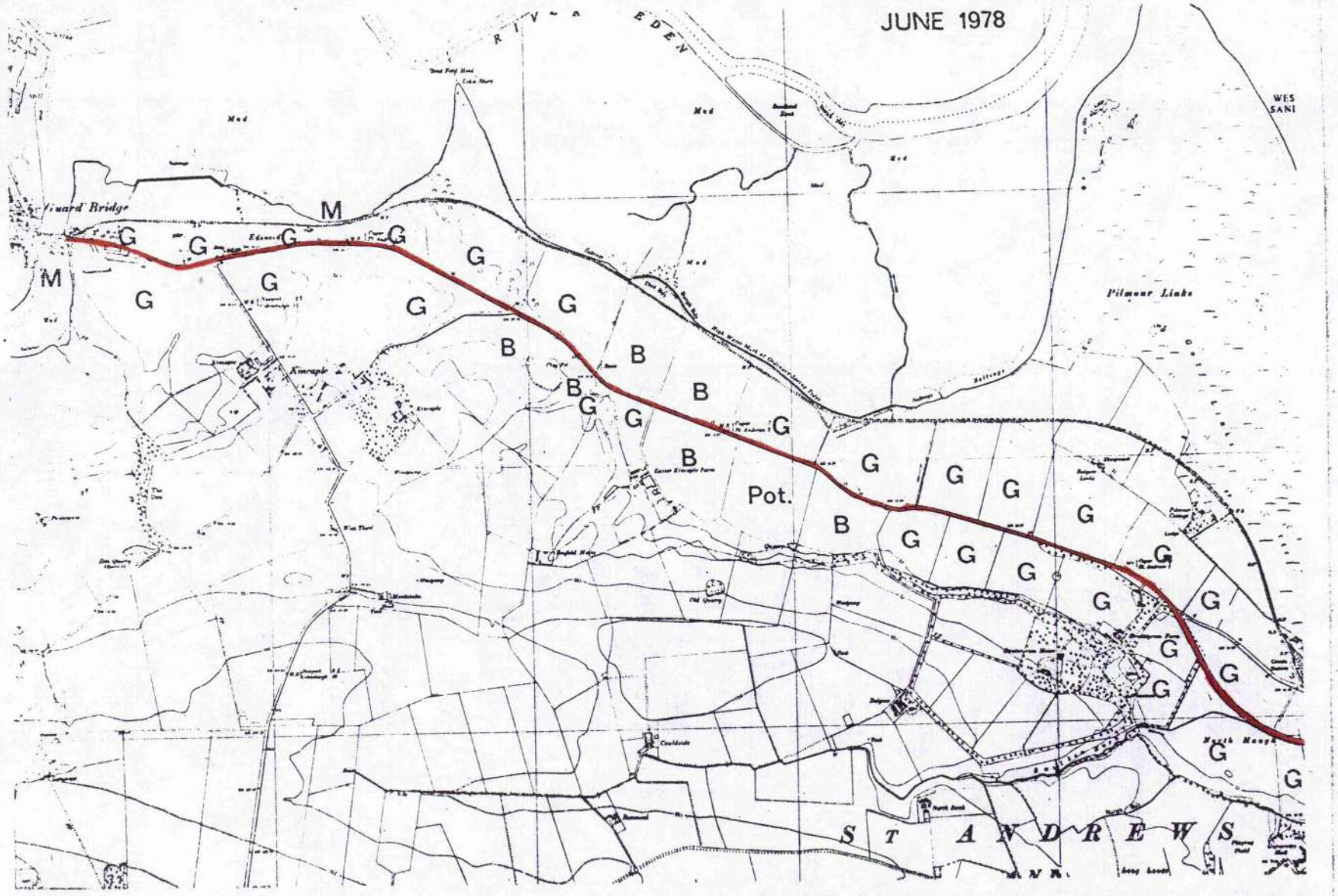


Figure 4.4 Map of the transect area showing field types present in June 1978.
G - grass; M - mud; B - barley; Pot. - potatoes.

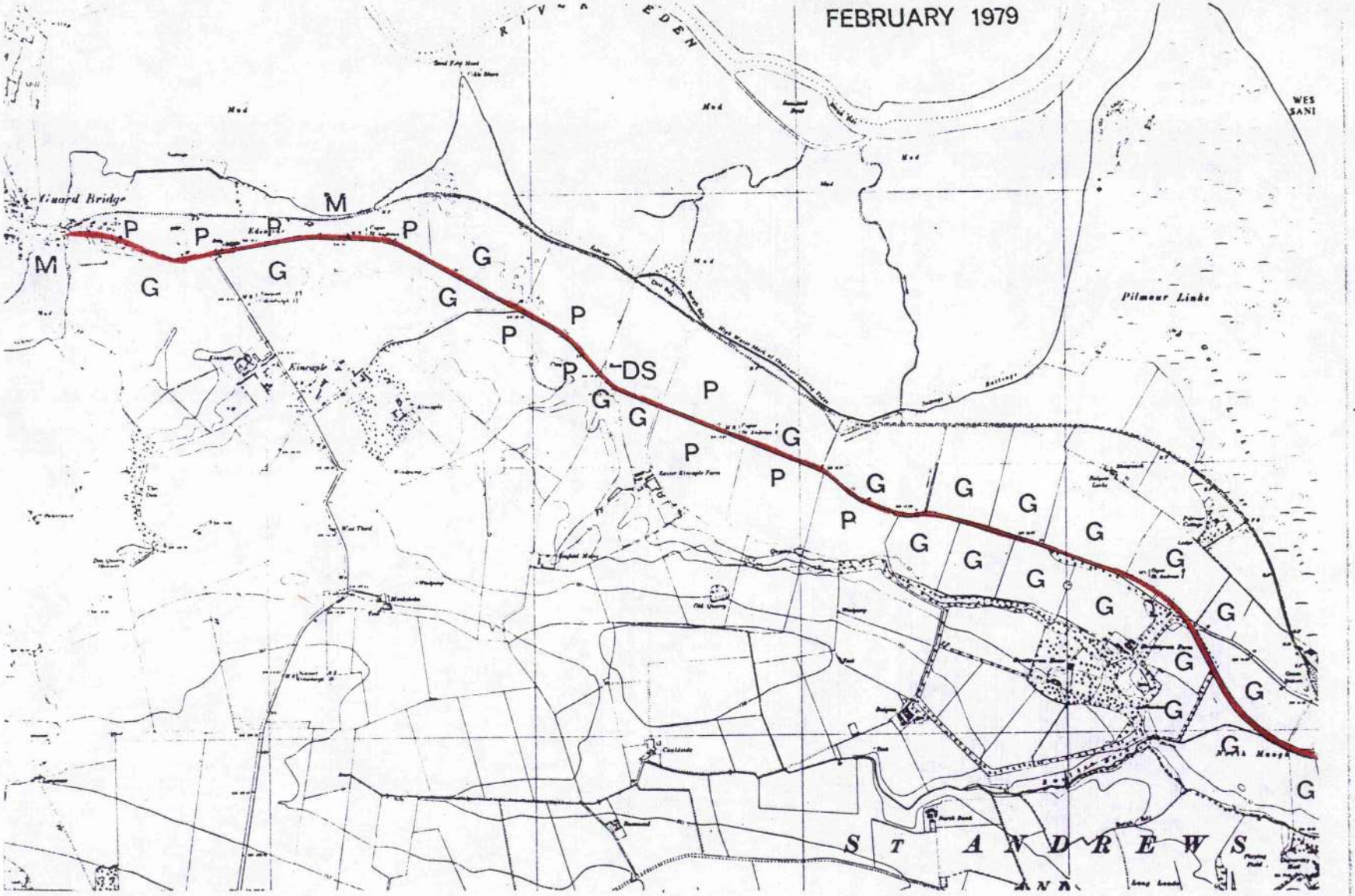


Figure 4.5 Map of the transect area showing field types present in February 1979.
G - grass; P - plough; M - mud; DS - dung stubble.

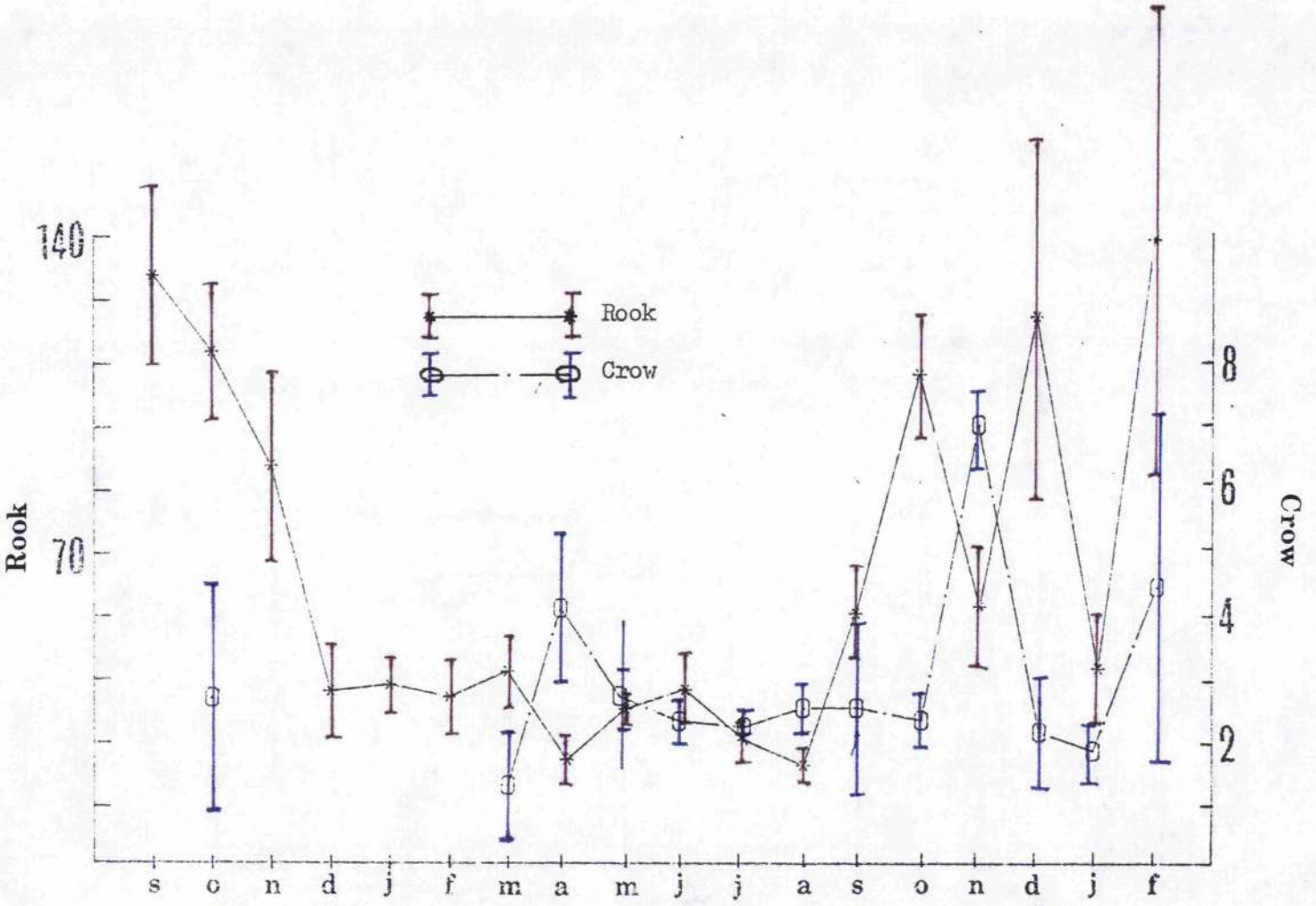


Figure 4.6 The average numbers of rooks and carrion crows seen per transect count in each month of the study. Vertical bars represent ± 1 standard error.

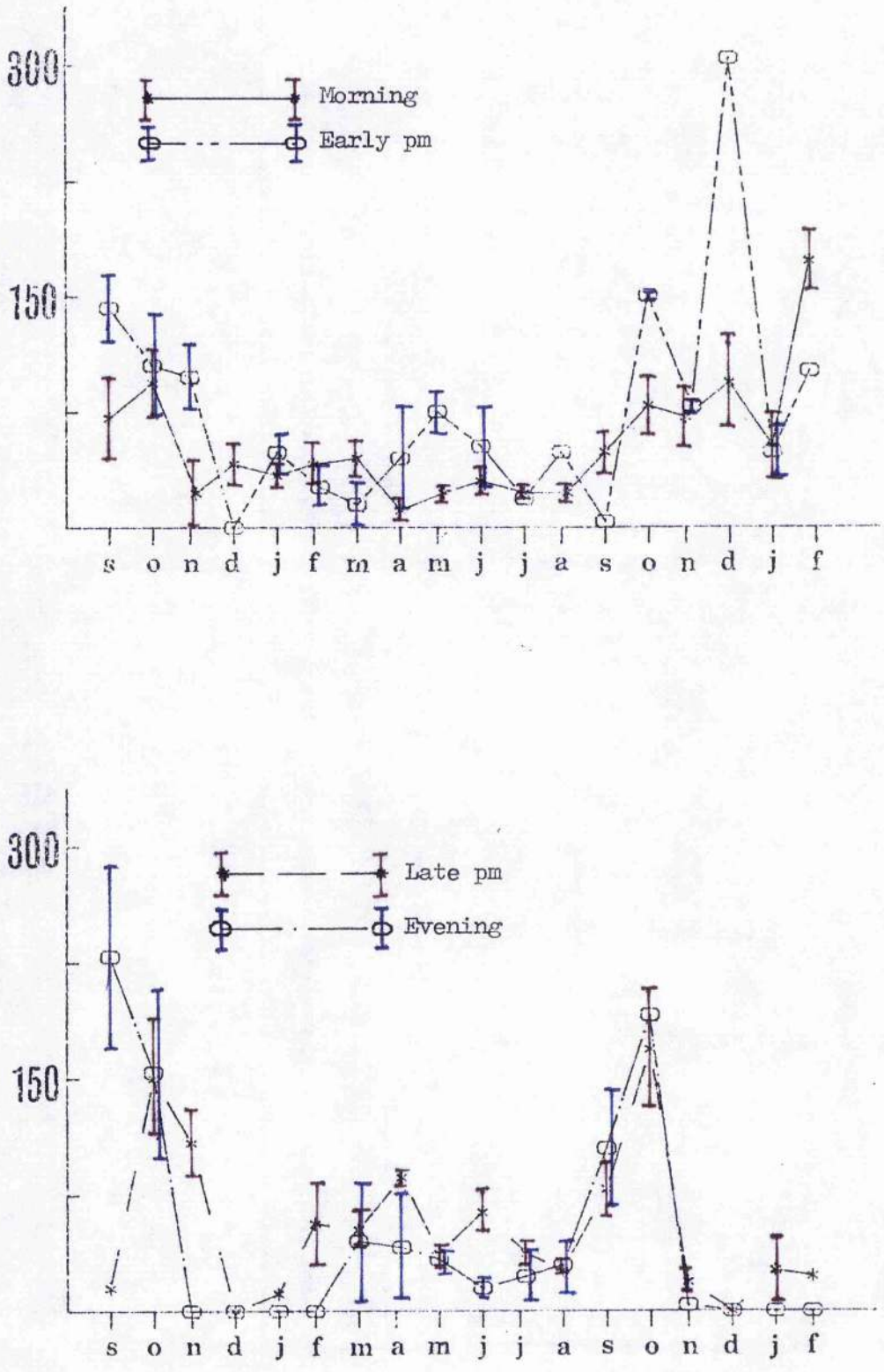


Figure 4.7 The average numbers of rooks seen at different times of the day in each month of the study. Vertical bars represent ±1 standard error.

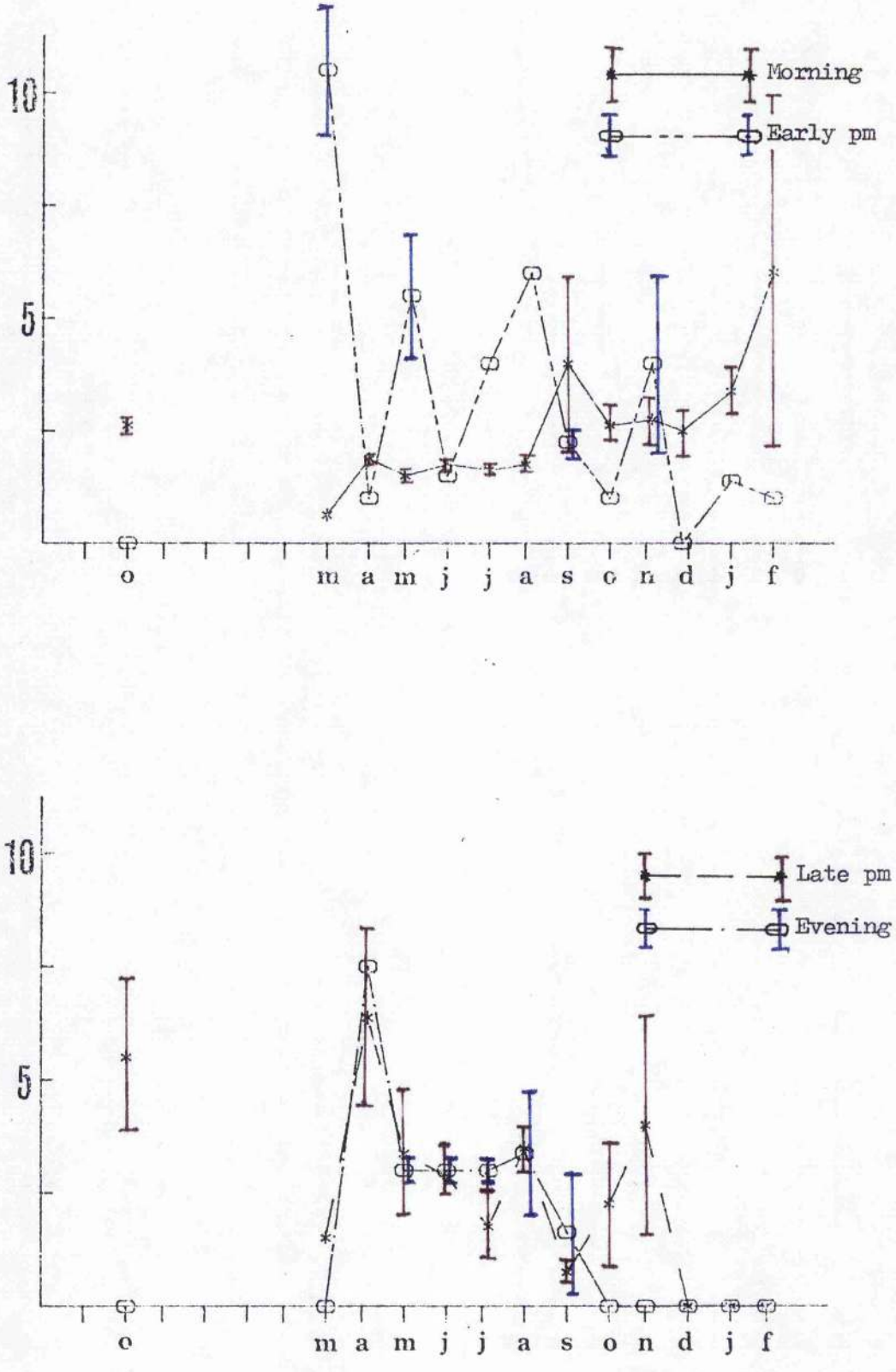


Figure 4.8 The average numbers of carrion crows seen at different times of the day in each month of the study. Vertical bars represent $\pm$ 1 standard error.

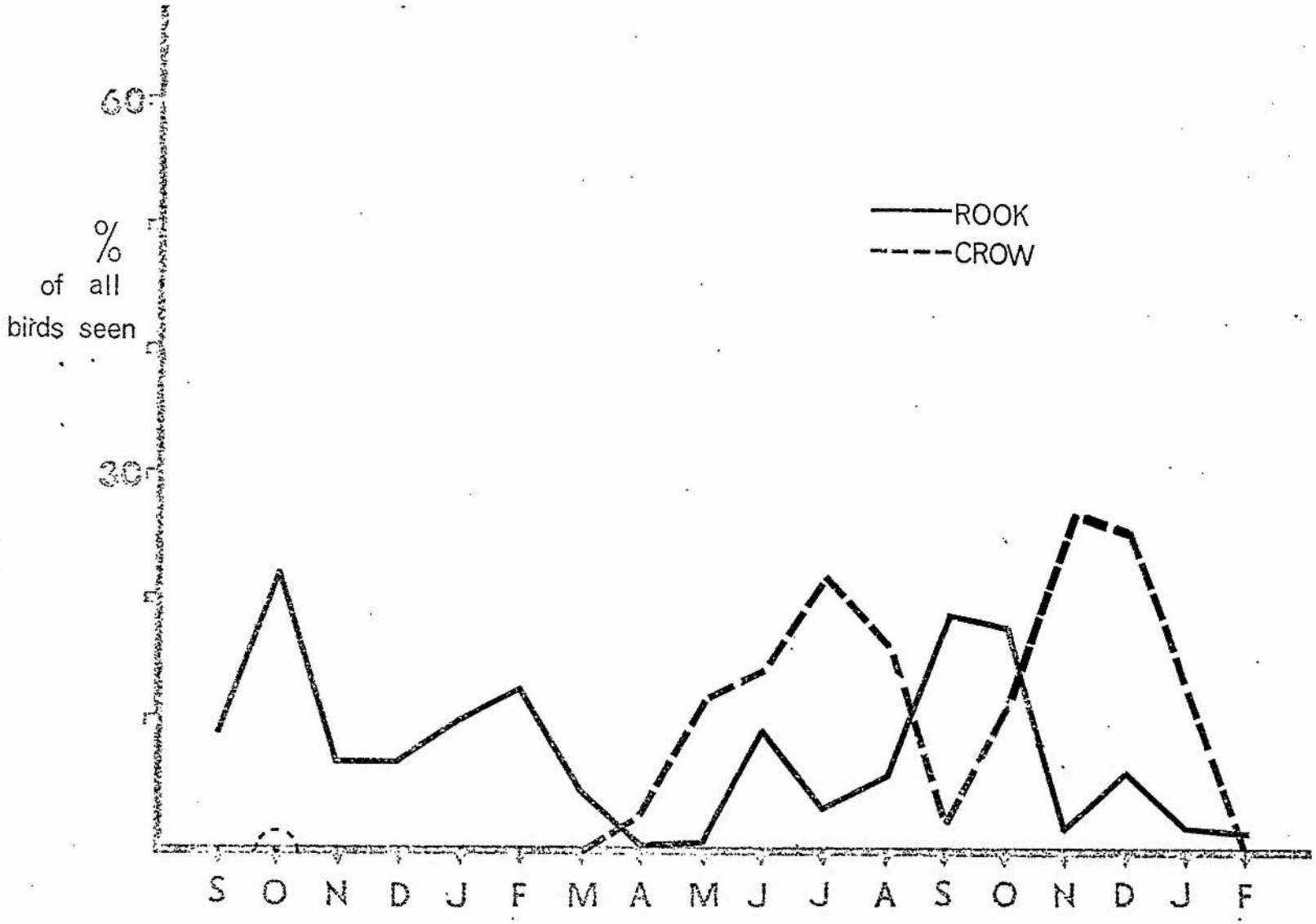


Figure 4.9 The proportions of all rooks and carrion crows seen which were resting in each month of the study.

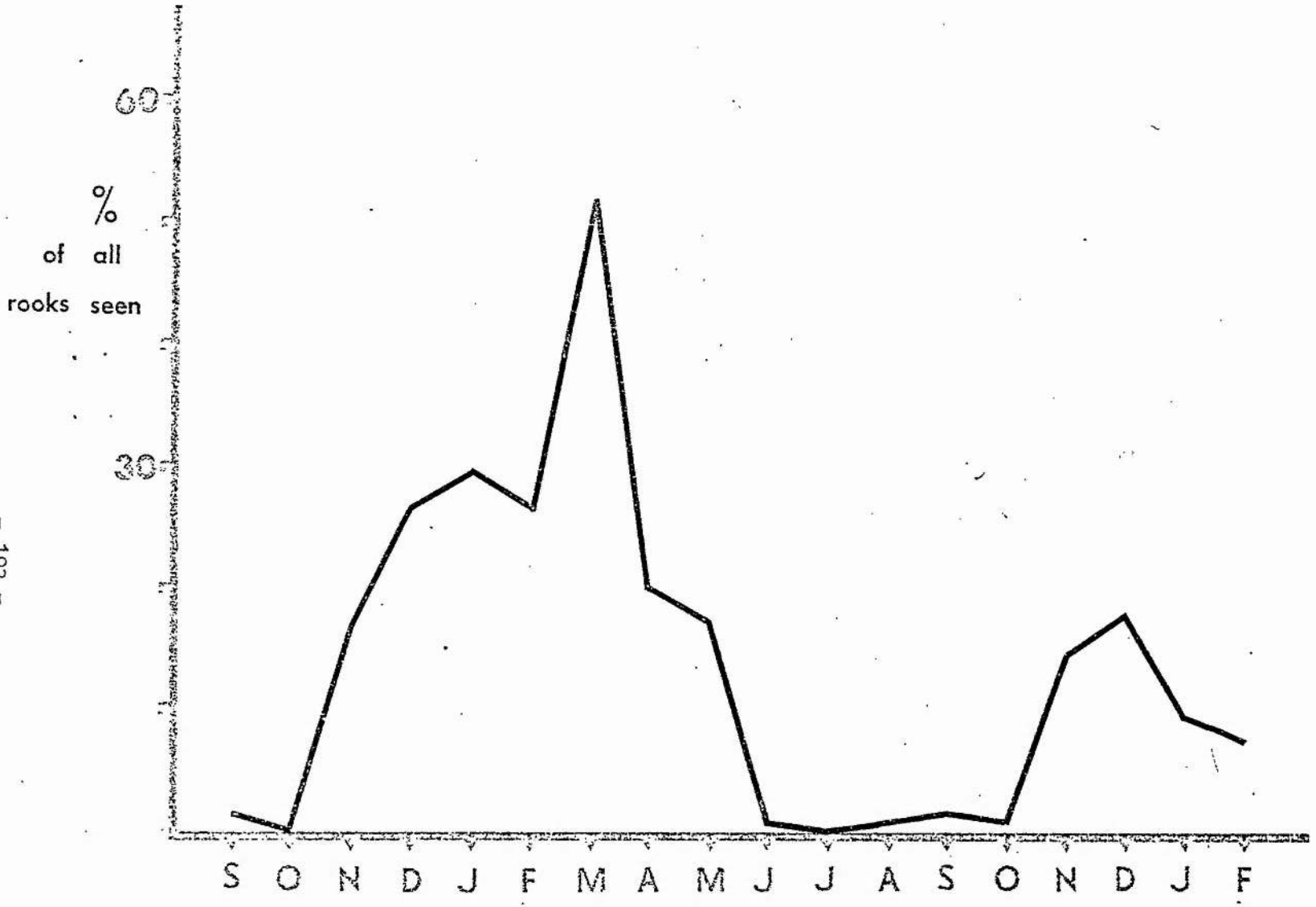


Figure 4.10 The proportions of all rooks seen which were in a rookery in each month of the study.

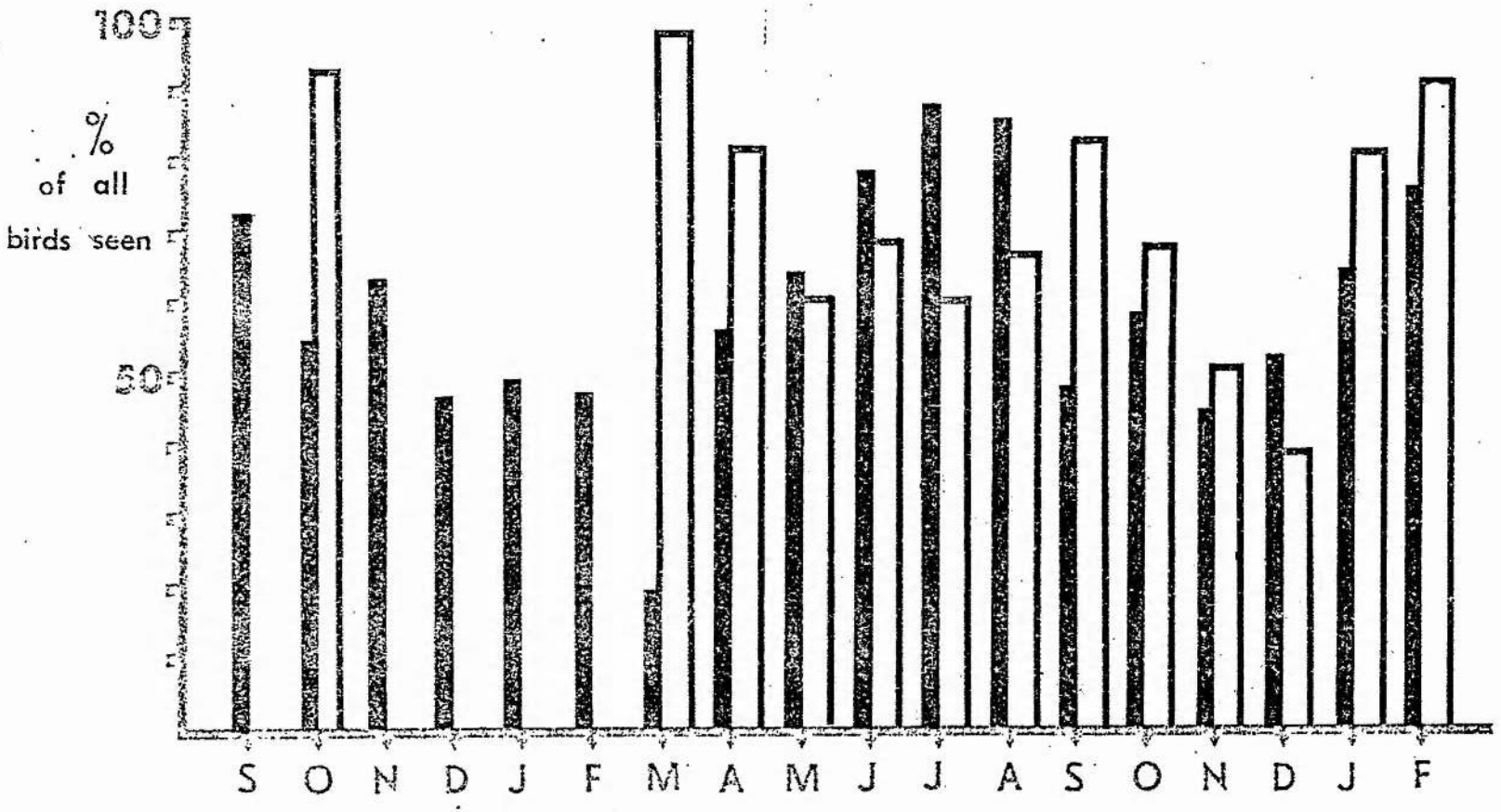
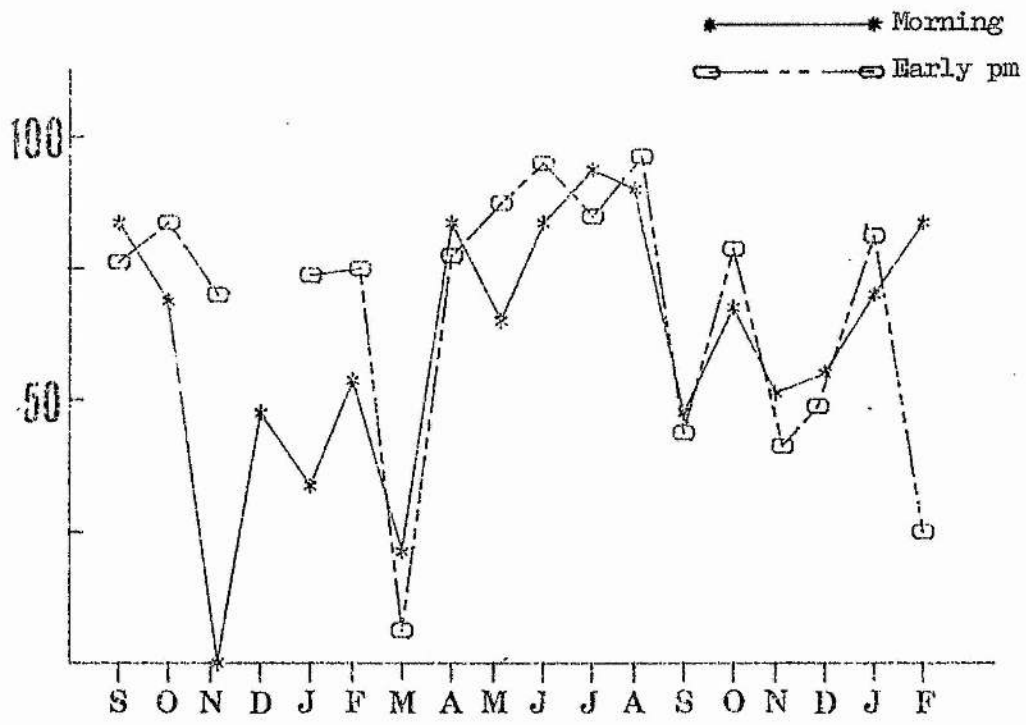


Figure 4.11 The proportions of all rooks and carrion crows seen in each month of the study which were feeding or foraging.



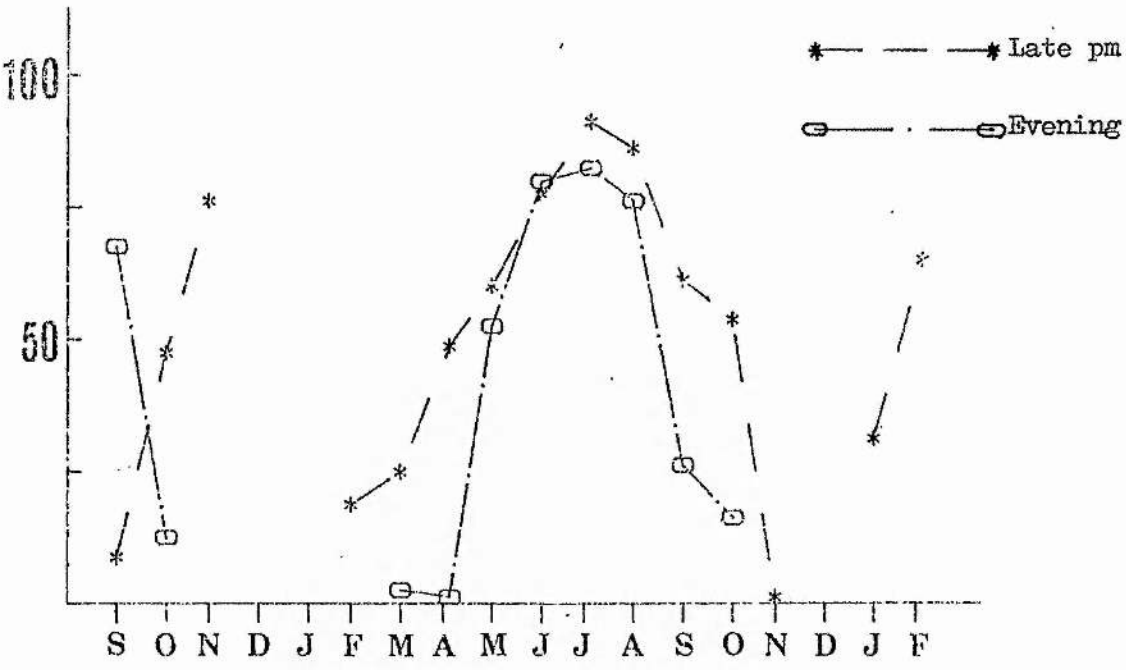
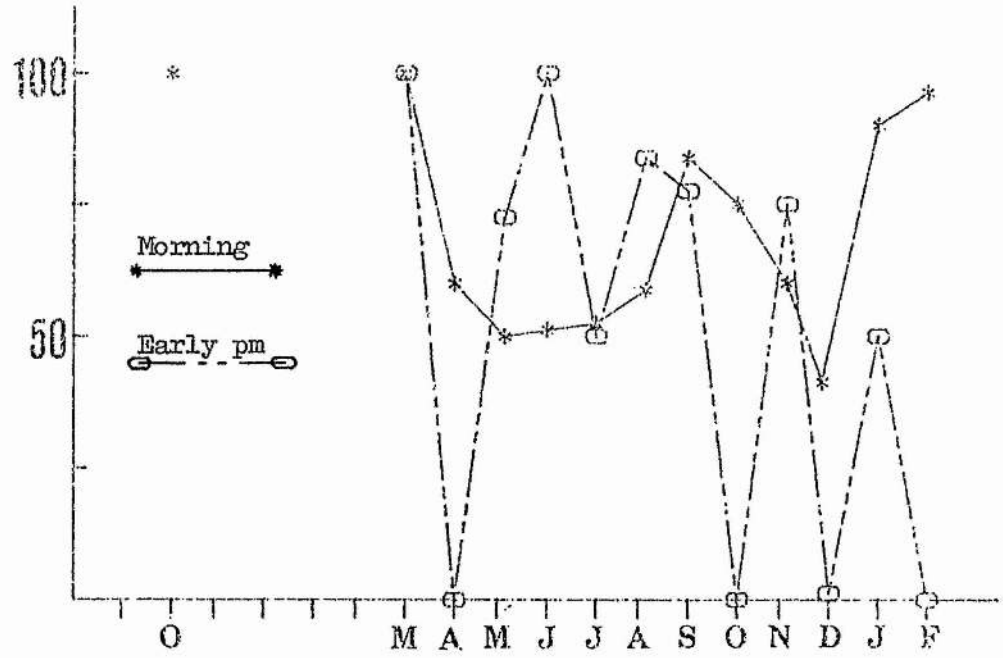


Figure 4.12 The proportions of all rooks seen which were feeding at different times of the day in each month of the study.



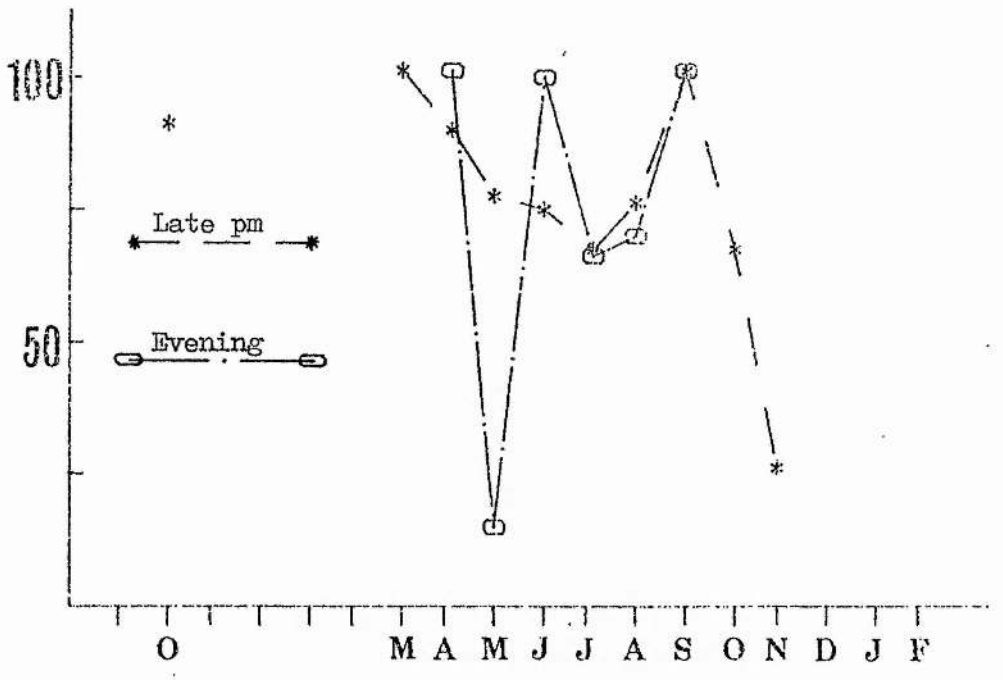


Figure 4.13 The proportions of all carrion crows seen which were feeding at different times of the day in each month of the study.

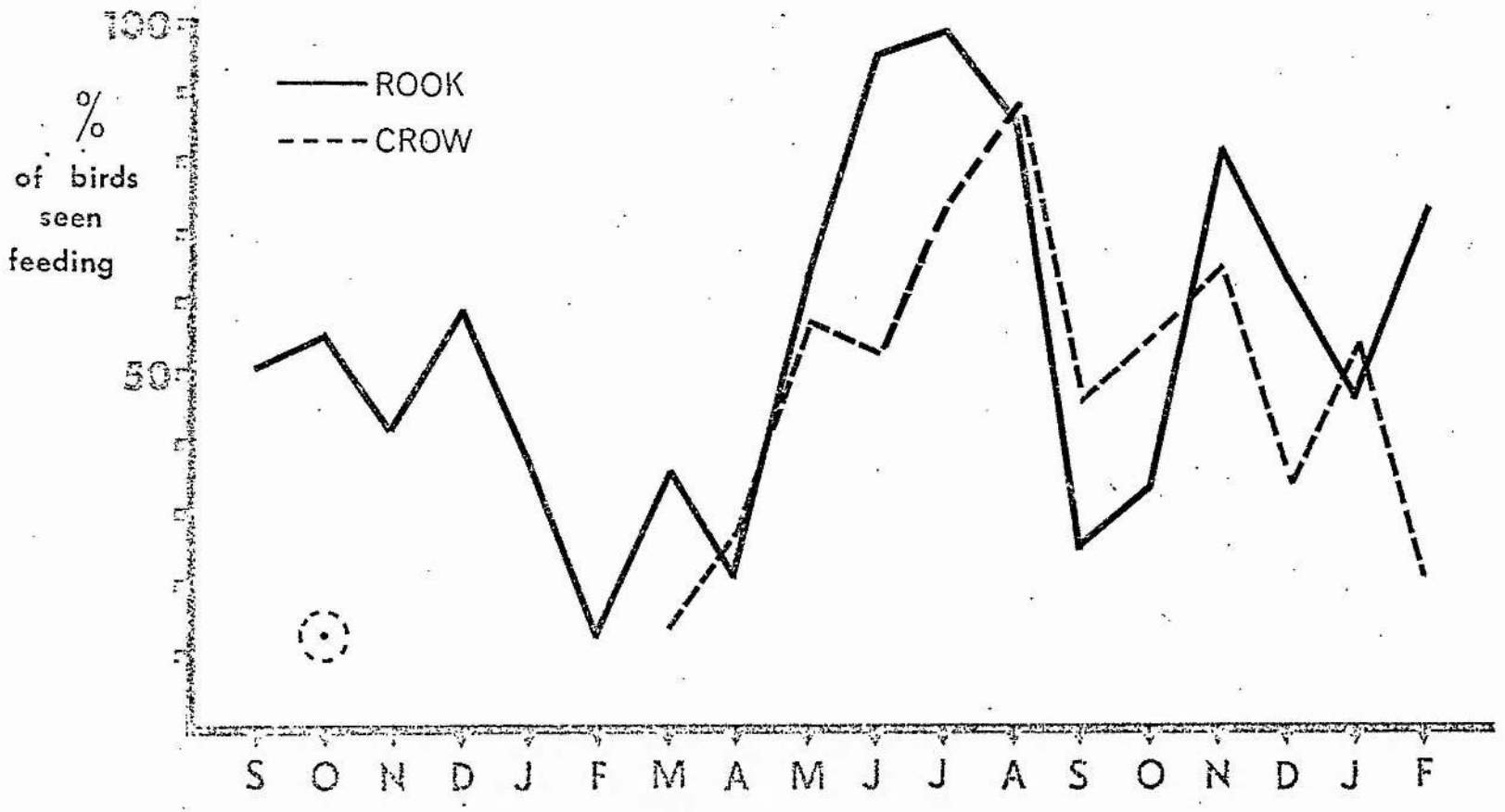
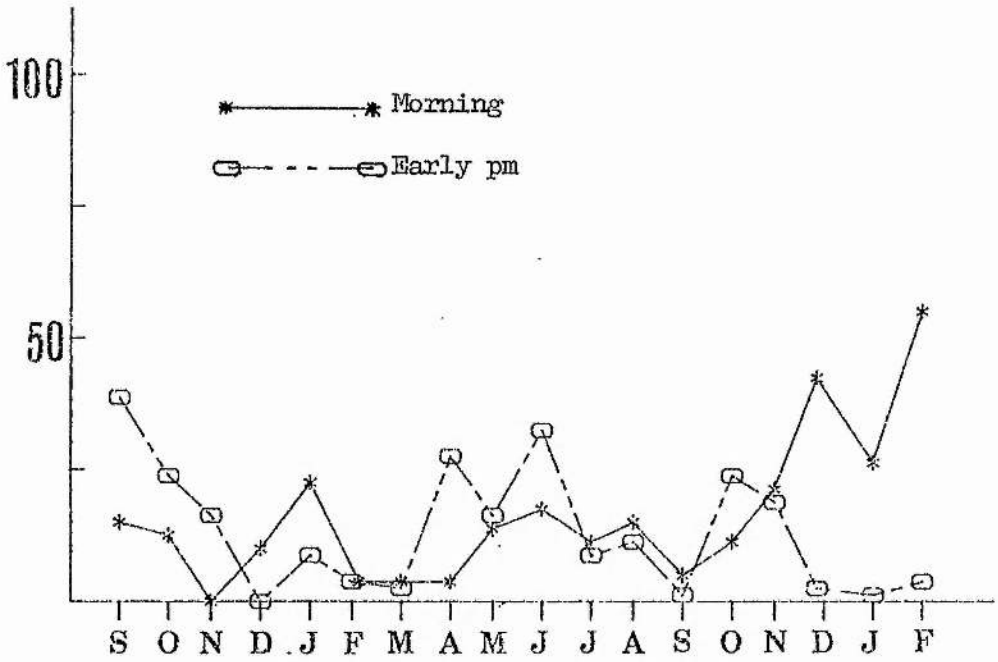


Figure 4.14 The proportions of feeding rooks and carrion crows which were doing so on grass fields in each month of the study.



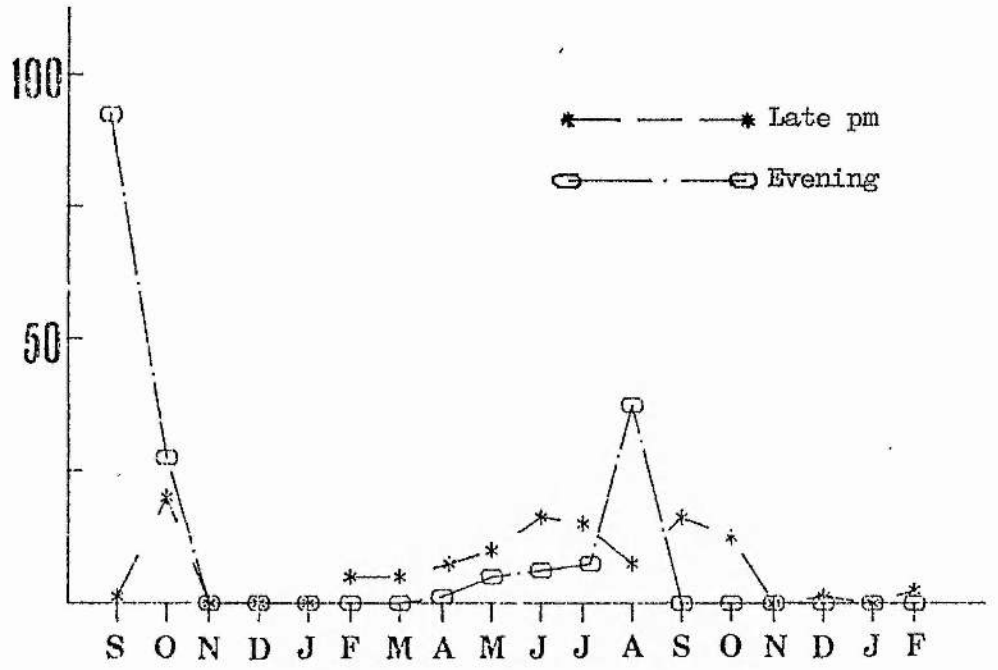


Figure 4.15 The mean flock sizes of rooks feeding on grass fields at different times of the day in each month of the study.

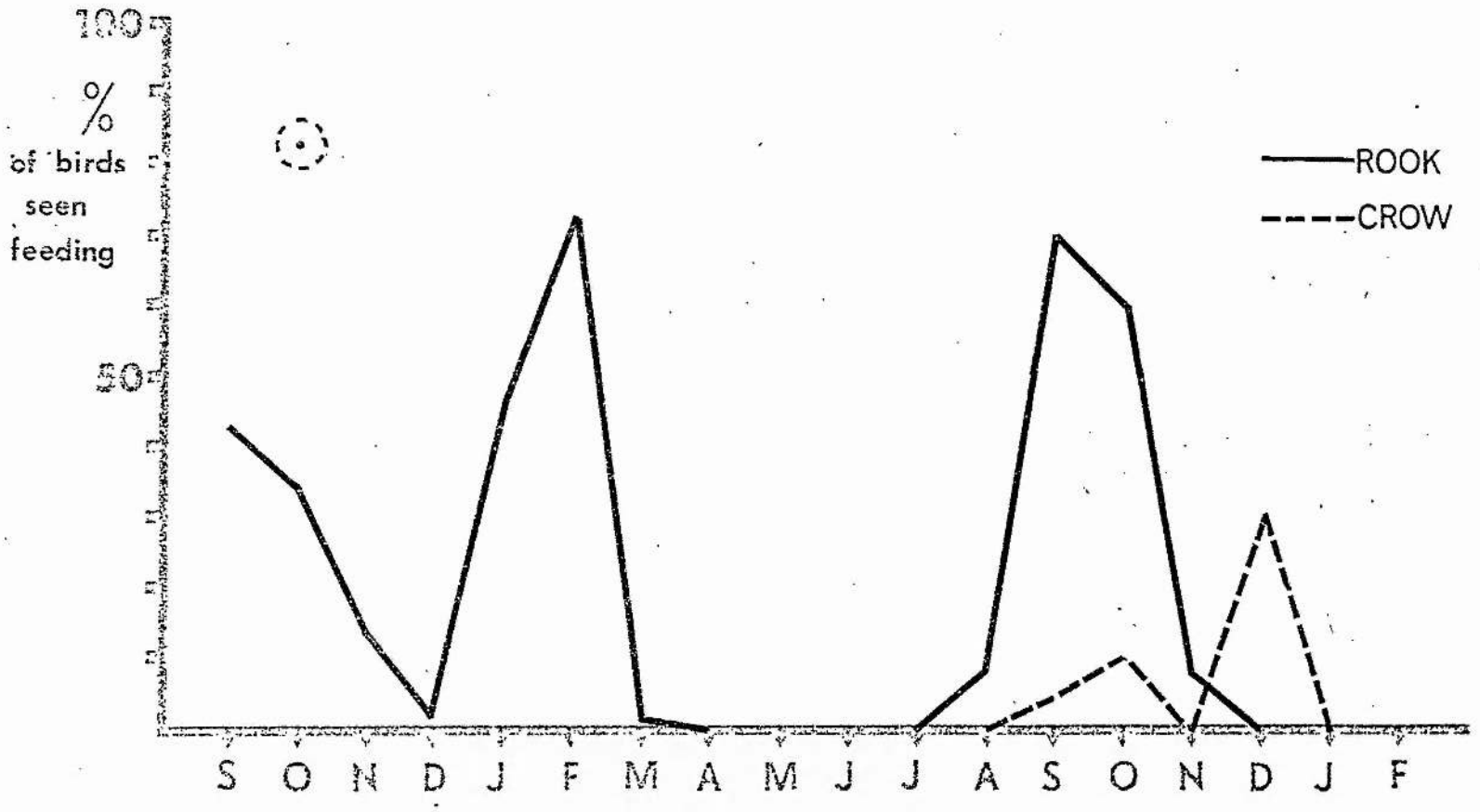


Figure 4.16 The proportions of feeding rooks and carrion crows which were doing so on barley stubble fields in each month of the study.

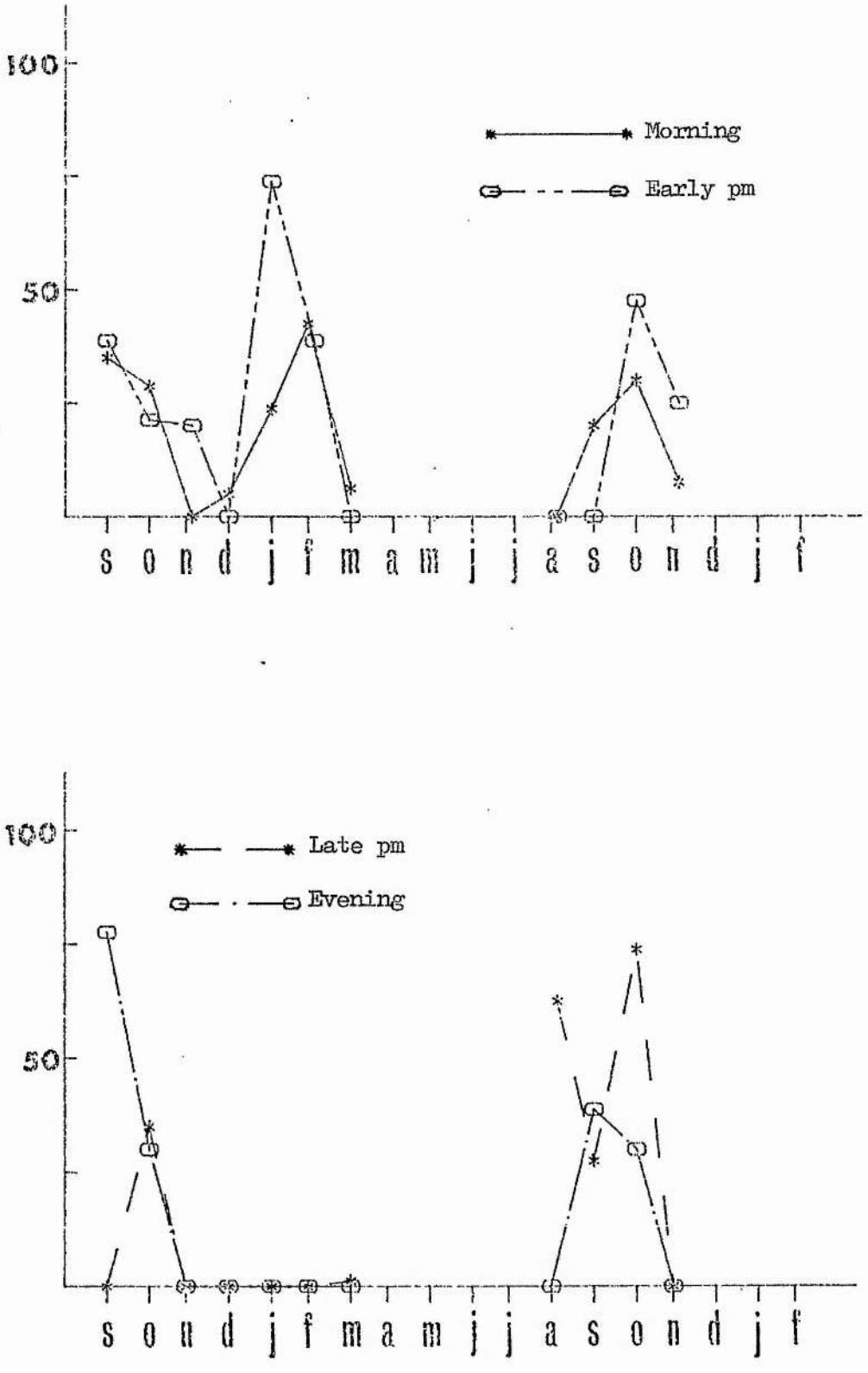


Figure 4.17 Mean flock sizes of rooks feeding on stubble fields at different times of the day in each month of the study.

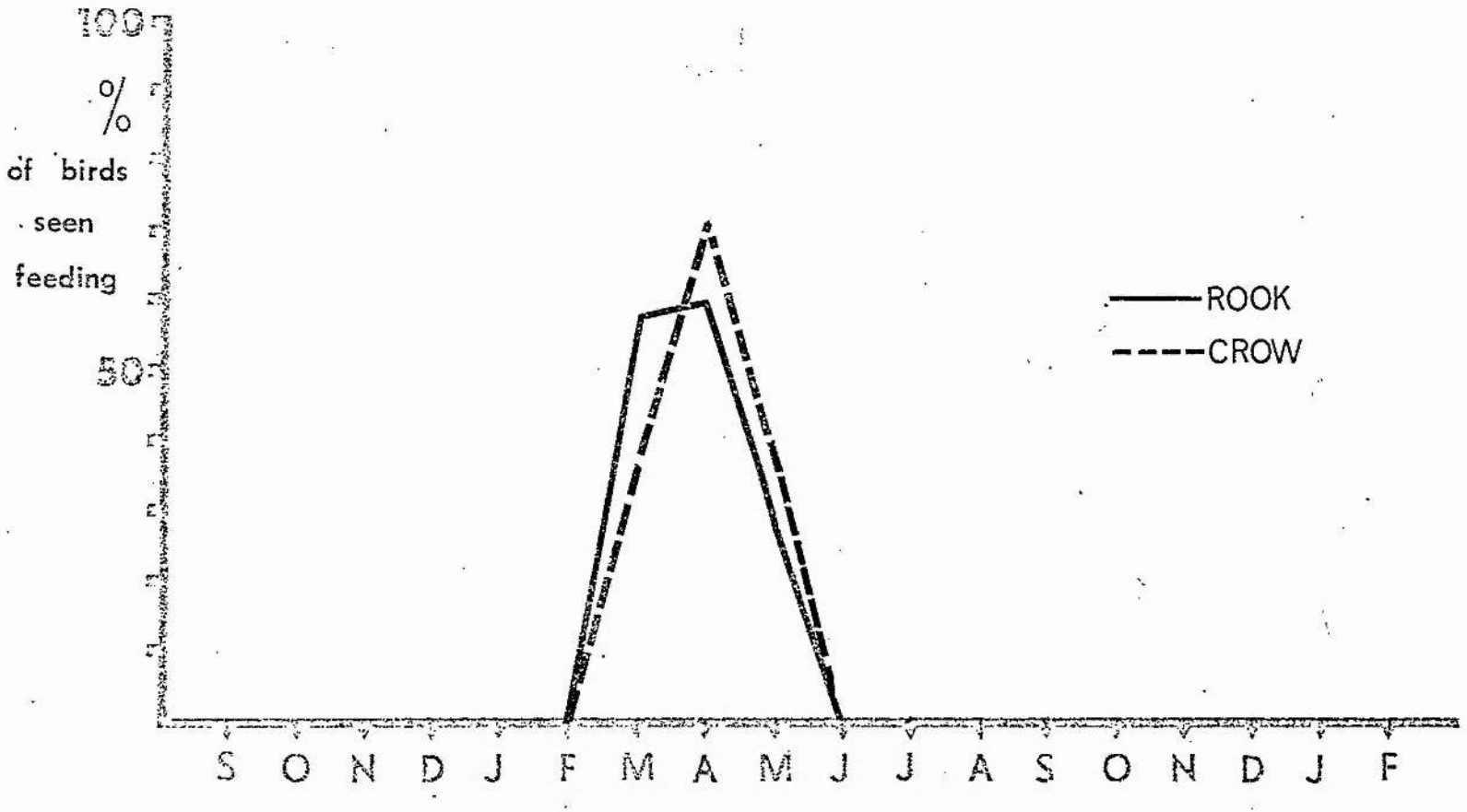


Figure 4.18 The proportions of feeding rooks and carrion crows which were doing so on sown barley and braird fields in each month of the study.

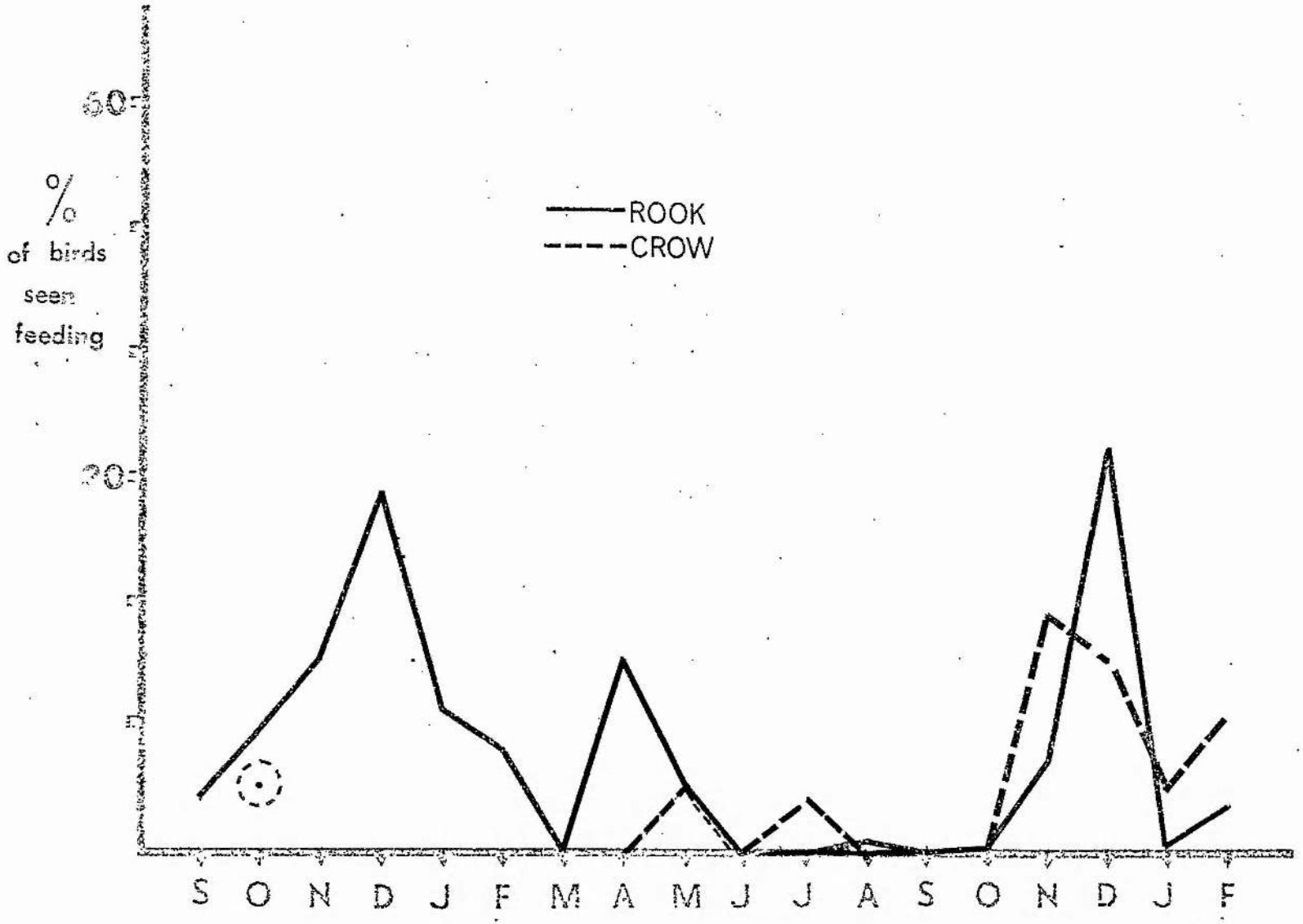


Figure 4.19 The proportions of feeding rooks and carrion crows which were doing so on ploughed fields (including those where ploughing was in progress) in each month of the study.

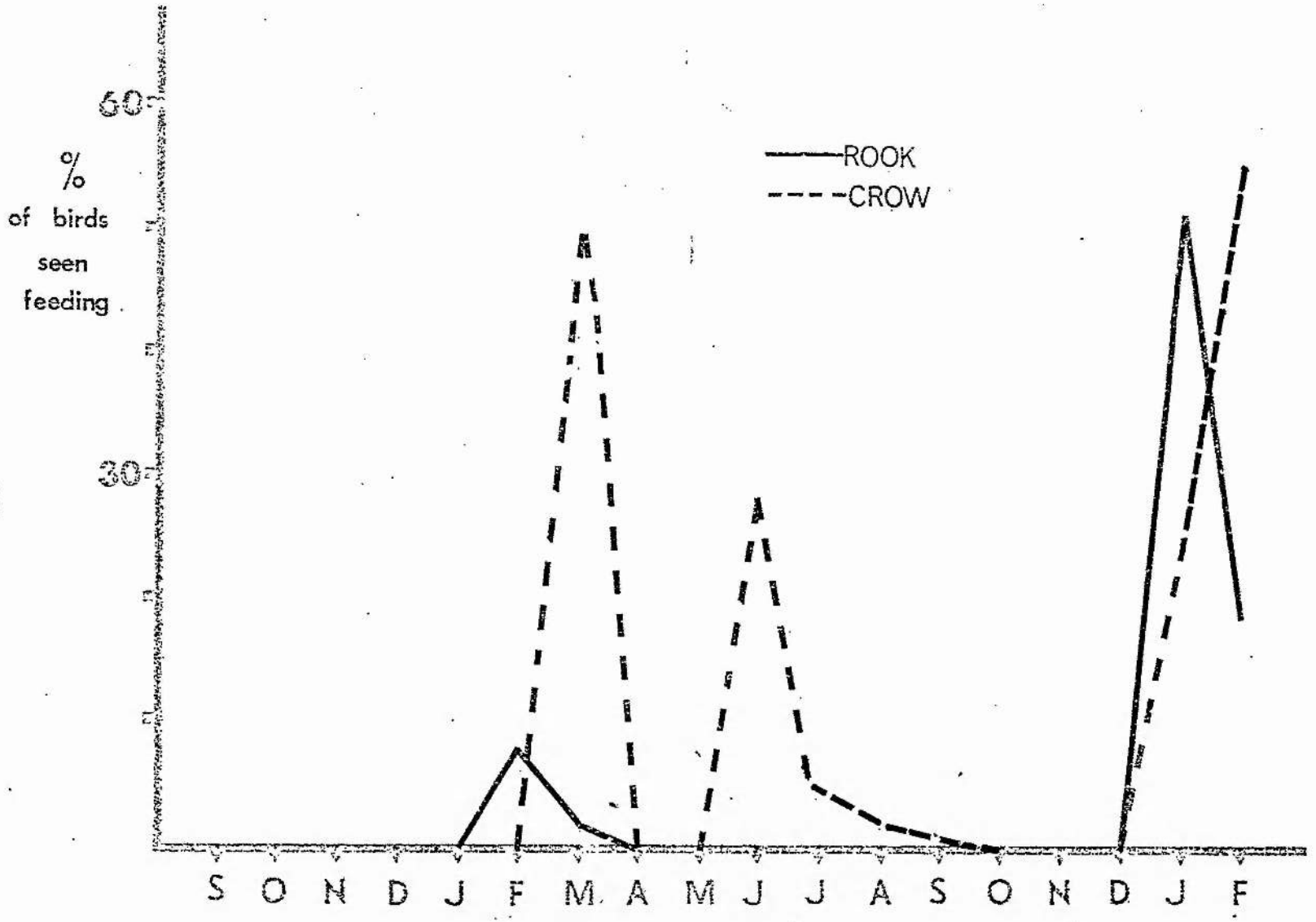


Figure 4.20 The proportions of feeding rooks and carrion crows which were doing so on dung heaps and dung covered stubble fields in each month of the study.

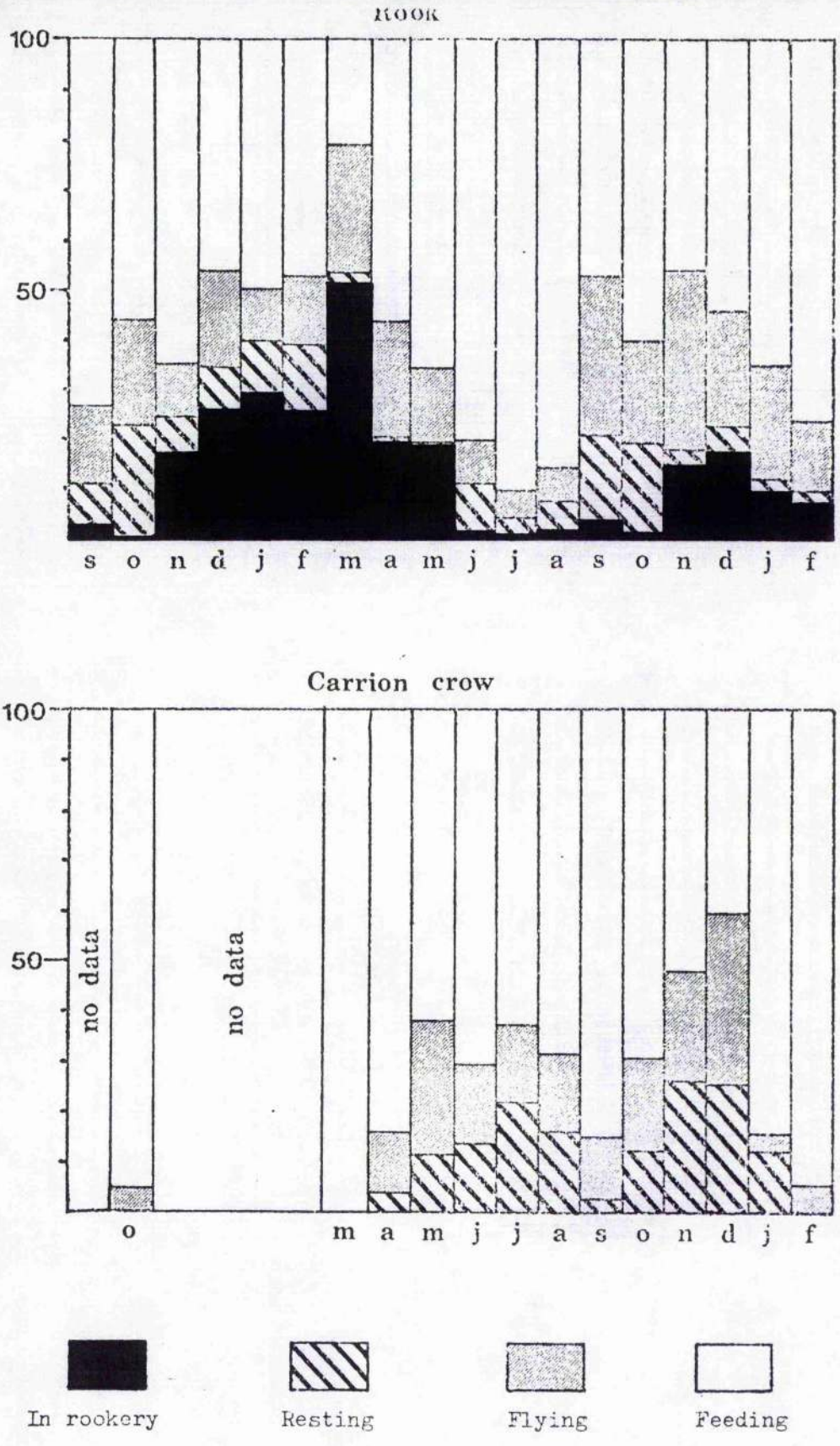


Figure 4.21 The proportions (% of all birds seen) of rooks and carrion crows engaged in various activities in each month of the study.

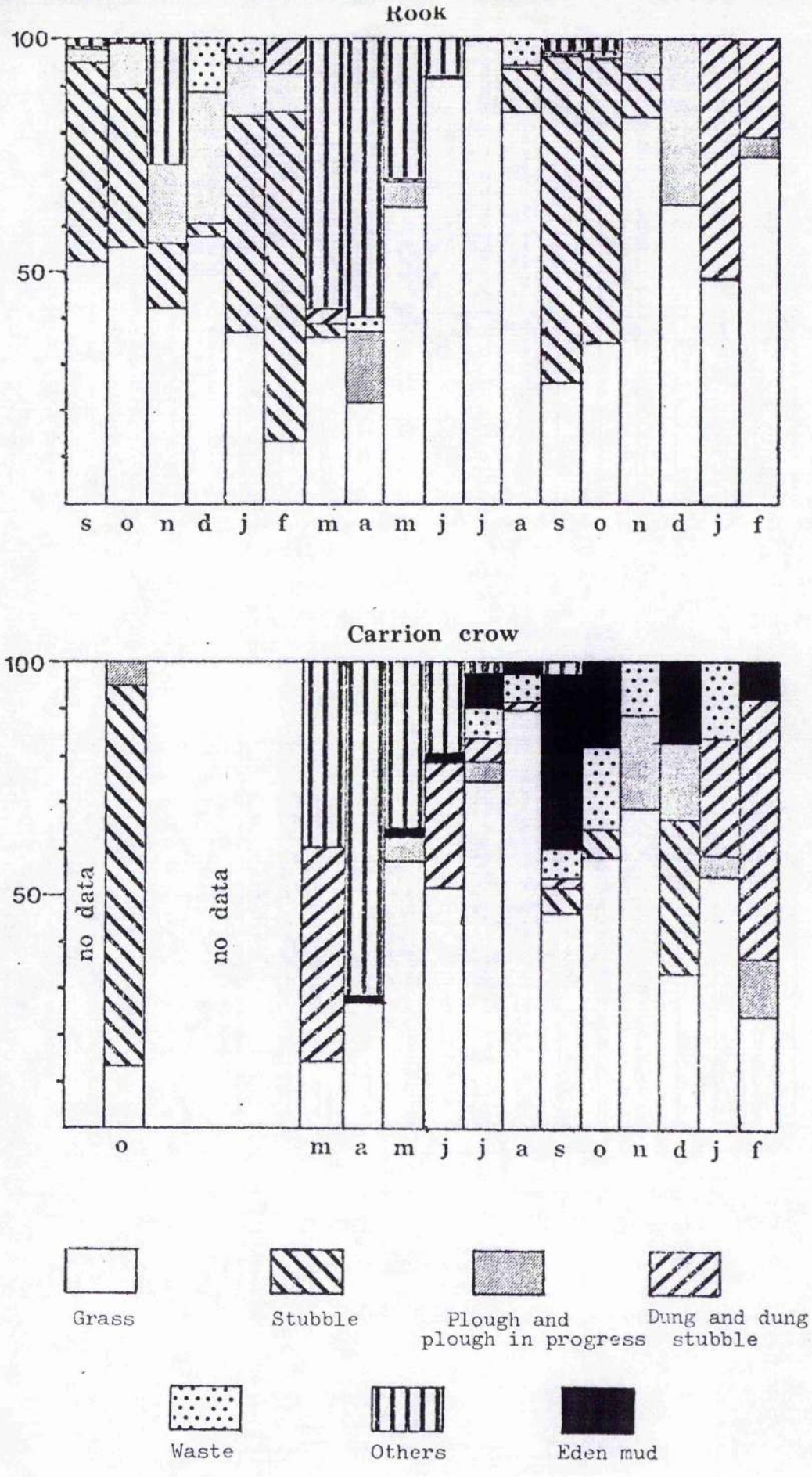


Figure 4.22 The proportions (% of feeding birds) of rooks and carrion crows feeding on the various field types in each month of the study.

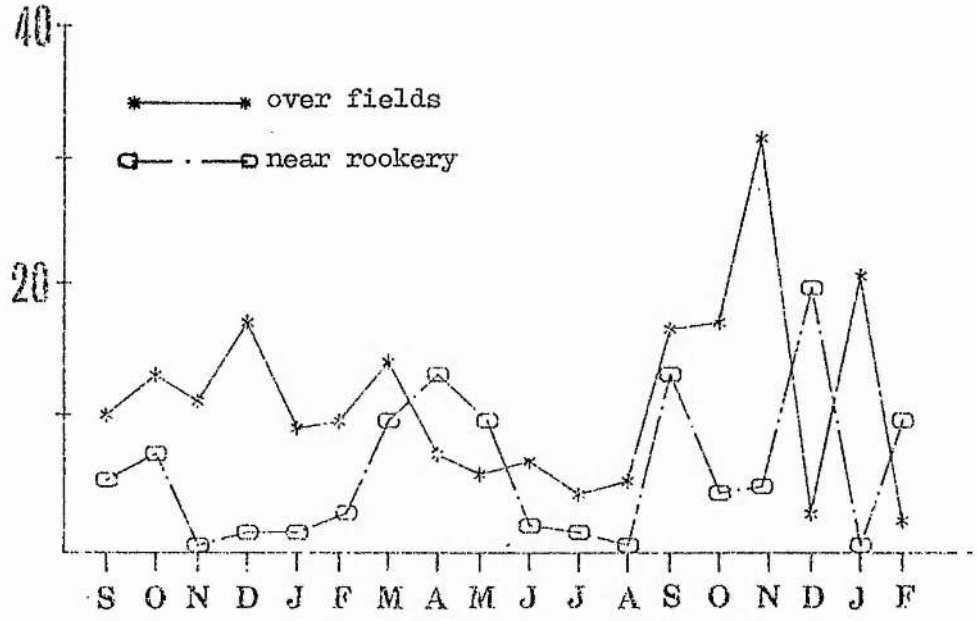


Figure 4.23 The proportions of rooks (% of all birds seen) which were flying either in (or near) a rookery or not near a rookery in each month of the study.

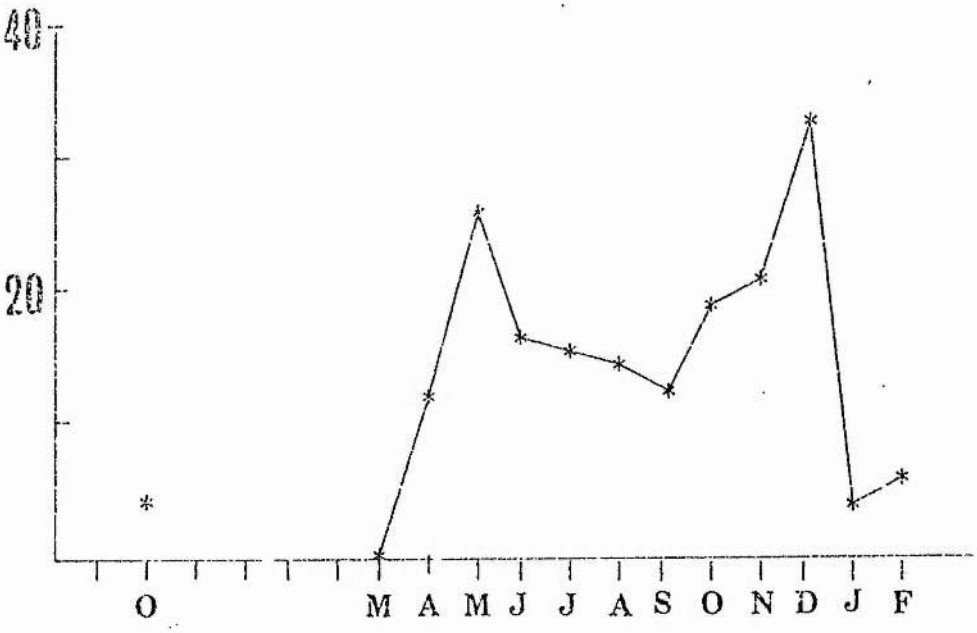


Figure 4.24 The proportions of carrion crows (% of all birds seen) which were flying in each month of the study.

Chapter 5. Niche metrics of rooks and carrion crows

INTRODUCTION

In the previous chapter the use rooks and carrion crows made of their habitats was described. Habitat therein was defined in terms of the way these species distributed themselves in the environment with little emphasis on intracommunity (Whittaker et al 1973, 1975) aspects of their existence. The present chapter develops further and more quantitatively the habitat use of these corvids, relating it to the availability of resource stations (field types) along the transect route. Also explored are some intracommunity attributes of the way these species distribute themselves, that is some components of their niches.

General methods

The data used in this chapter are those of the previous chapter, i.e. the results from the transect counts. The total area of the transect area was just under 265 ha and, as mentioned in the previous chapter, all parts of it were continuously monitored for changes in crop types. The area of each discrete part of the whole transect area, comprising the various resource stations, was calculated for the duration of the study. This was done by tracing the outline of each of them (usually fields) on to card from the 1:25000 Ordnance Survey map of the area and weighing each of the resulting card shapes. These were then compared against a standard 2.54 x 2.54 cm (1 x 1 in) square shape of known weight and representing a fixed area, and the appropriate transformations made to derive the field areas. This method was suitable for most of the resource stations included along the transect route, but was not for

animal feed troughs, sheep, stacks or dung heaps, as these were unpredictable in their appearance both temporally and spatially. Feed troughs and sheep, as they were rarely present, were therefore each given nominal values of 0.01 ha as their average monthly abundance during the study, while the more abundant stacks and dung heaps were each given a value of 0.1 ha. The abundance of mud was determined using the above method and dividing the resultant figure by 2 in order to compensate for tidal fluctuations.

A SIMPLE INDEX OF HABITAT UTILISATION BY ROOKS AND CARRION CROWS

The simplest index of utilisation of a resource station by a species is the one derived when the relative number of animals using the resource station is divided by some measure of the relative abundance of the resource station. Thus the utilisation of available field types by rooks in Aberdeenshire was determined by dividing the percentage of the total number of rooks seen feeding on each field type by the respective percent abundance of each field type (Dunnet & Patterson 1968). As pointed out by Duncan (1983), who used this method to gauge the habitat preferences of horses, this index can vary from 0, signifying avoidance of a resource station, through 1, signifying use of a resource station in direct proportion to its abundance, to higher values signifying increasing preference. Although the indices derived will give an indication of the relative amount of use of different resource stations, they will not necessarily indicate the relative amounts of food captured in each of them (Dunnet & Patterson 1968).

Tables 5.1 and 5.2 (pp. 230-235 and 236-241 respectively) show the monthly indices calculated for the use of all field types in the transect area from September 1977 to February 1979 for the rook

and the carrion crow respectively. There is an important difference between these tables and the corresponding one given for the rook by Dunnet & Patterson (1968). In their calculation of the index of utilisation the abundance of a crop type was defined as the number of fields under that crop expressed as a percentage of the total number of fields in the study area. In the present study, though, the abundance of each crop type was calculated as a percentage of the total area of the transect area. Therefore, differences in the size of fields in the Aberdeenshire investigation could have affected the values of the indices derived, but this is not a problem in the present case. Despite this, however, the results from the two studies are remarkably similar. Dunnet & Patterson (1968) found a preference for grass fields in summer and, to a lesser extent, in winter. This is the same pattern as found in Fife. Sown grain was preferred, when available, in both Aberdeenshire and in Fife, but stubble was not preferred to the same extent in winter in Fife as it was in Aberdeenshire. A possible reason for this is that only barley stubble was available in Fife, whereas other cereals, notably oats, were available in Aberdeenshire (Feare 1974). This may also account for the preference for ploughed fields by Fife rooks in winter, while there was no preference for them by Aberdeenshire rooks at this time of year. Rooks certainly prefer oat grains to barley grains (personal observation, Luniak 1977), the reason for this being that oats are easier to de-husk. However, if dung covered stubble fields are considered the preference for stubble is apparent in the winter. Braird fields were at no time preferred by either Fife or Aberdeenshire rooks. No consistent preference for other field types was found in the present study.

Carrion crows preferred to forage on grass fields at the same times as rooks, although there was a stronger preference for

grass in winter and a weaker one in summer (Table 5.2, pp. 236-241). When available, stubble fields were not preferred by carrion crows to the same extent as by rooks - they only showed a preference for this field type in two months. As with rooks, carrion crows preferred to forage on sown barley fields when they were available, but they also, unlike rooks, showed a preference for braird when it was available. Carrion crows preferred to forage on ploughed fields for little of the periods they were available and, as mentioned in the previous chapter, never foraged on such fields when a tractor was present. Although the River Eden estuary bed (mud) was available throughout the study carrion crows preferred to forage on it for only a few months. By far the strongest preference of crows was that for dung (heaps and dung covered stubble). In all months when this foraging station was present they utilised it heavily.

It is notable that in the summer both the rook and the carrion crow switched from having no preference for grass fields to preferring them at about the time the young were leaving the nest (June for rooks, July for crows). In addition, the carrion crow developed a wide range of preferences in July which included plough, dung, mud and waste. This would seem to suggest that when the young rook leaves the nest and follows its parents to feeding grounds it is learning most of its initial feeding techniques on grass fields, whereas the young carrion crow is obtaining a wider range of experience with respect to field types. Clearly, then, the advantage which will accrue to a young carrion crow will be that it becomes familiar with many characteristics of its habitat which will enable it to survive better in the future. The advantage to rooks of a restriction of habitat preference at this time is less clear. In times of low population density some species of birds only utilise preferred or optimal parts of their habitat due to a relaxation of

intraspecific competition. The observation which results is a restriction of habitat preferences (Partridge 1978). This is unlikely to be the case with rooks though. Population density, of course, is highest just after the breeding season, and an expansion rather than a contraction of habitat preferences would be expected. Furthermore, such an expansion took place soon after the breeding season when population density was presumably declining due to juvenile mortality. A possible explanation of the reduction in the number of preferred field types by rooks in the summer could be provided by a consideration of interspecific effects. Svardson (1949) suggested that when there is a high degree of interspecific competition then a species should narrow its choice of habitat to the "most optimal". Willis (1966) developed this further and pointed out that other species may increase the diversity of use of their environment. Given the wide range of habitat preferences of carrion crows at this time, then rooks may have been restricting their preference in order to avoid potential active competition with carrion crows. The effects of such competition will be more severe for a rook at this time of year as the young will be less able than the adults to defend themselves during agonistic interactions with the larger, more powerful corvid. If the rook normally circumvents such contact by seeking 'safety in numbers' or via 'swamping' (Rowley 1973) then the fact that the average size of rook flocks at this time of the year is small (chapter 4, Table 4.6, pp. 168-169) is consistent with this interpretation. Interestingly, rook flock sizes were smallest during March, April and May 1978 (Table 4.6, pp. 168-169) - also times when rook habitat preferences were restricted (only one field type preferred in March and May, Table 5.1, pp. 230-235). Carrion crow habitat preferences also were narrower at these times, however, so perhaps other factors had a common effect on

the two species. Further treatment of differences in the niche breadths of the two species at different times of the year is given later with regard to specific hypotheses.

NICHE BREADTH AND OVERLAP OF ROOKS AND CARRION CROWS

Definition of some terms

The definition of niche alluded to in the previous chapter, to reiterate, referred to the intracommunity role of a species (Whittaker 1973, 1975). That is, it considers the role of a species in a community in relation to, amongst other factors, other species. Vandermeer (1972) recognised three different, but related, types of niche. First of all there is the fundamental niche of a species, defined as the niche a species would fill if no other species, including the species being considered, were present in the environment. Secondly there is the partial niche, which is the niche filled by a species when a number of other species are present in the environment. So in the presence of one other species one would speak of the first partial niche of the species in question, in the presence of two other species the second partial niche, and so on. Thirdly, the realised niche of a species is the niche filled by that species in the presence of all other species in the community. This is equivalent to the Mth partial niche of the species when there are M other species in the community.

Clearly this formulation is somewhat theoretical. For example, one can never know the true fundamental niche of a species. Nor can we define in any but the most rigorously controlled observations the various partial niches of species. The most obvious candidates for study under natural conditions here would be ecological succession on islands - a time consuming process, or the

comparison of many different environments, each having slightly different species profiles. Even here, though, the different environments would have uncontrollable variations in other components of niche such as weather variables, making quantitative comparisons an awesome undertaking. The most pragmatically meaningful construct is the realised niche, but even here we can never be quite certain that the M observed or arbitrarily fixed set (see below) of species in a community is the theoretical or prevailing maximum. Despite these drawbacks Vandermeer's (1972) formulation is useful as a working model with which to begin describing and quantifying the relationships that exist between species in the environment.

One other term requires to be defined here and that is community. Vandermeer (1972) defined it as an arbitrarily specified set of species in the environment. In the present context, then, the term intracommunity refers to the set of species composed of rooks, carrion crows and all other species of bird using the transect area, though what follows is really a consideration of the subset of this community which includes rooks and carrion crows, i.e. an arbitrarily fixed subset of two species. This is not to ignore the fact that the other species present in the environment are important in determining the partial and realised niches of the rook and the carrion crow. It helps, though, in making more explicit the ecological relationship between rooks and carrion crows in a particular environment (i.e. the transect area). In more operational terms, what such a treatment will facilitate is the specification of the partial niches of these two species with respect to each other, though it must be borne in mind that these partial niches are probably themselves the result of relationships with other species in the transect area. That is, they should not be regarded as first order partial niches. There is no evidence available in order to specify to which degree these partial

niches have reached - this would require knowing the total number of different species using the transect area. Nor is there any way of knowing at present whether or not it is the two species realised niches which are being compared. Many other species of bird used the transect area at different times of the day and year, and mammals also may have an effect on the realised niches of rooks and carrion crows.

Associated with these concepts are two components of niche which will be investigated here. These are niche breadth and overlap. Niche breadth refers to the diversity of resources (in the present case resource stations) utilised by an organism. For example, if a species utilises only one of ten available resource states it would have a narrower niche breadth than another species which utilises all ten. Animals with broad niche breadths may be called generalists, whereas those with narrow niche breadths are specialists. Niche overlap between different species is simply a measure of the similarity in resource utilisation of those species. Indices of niche breadth and overlap may be computed not only from observed patterns of habitat use but also from other aspects of species' ecology such as diet and feeding techniques. They are extremely useful in allowing quantitative comparisons to be made between different species in the same environment and also between the same species in different parts of its range. If two species show a high degree of habitat overlap it does not necessarily follow that they are competing with one another. Several authors have made this point (e.g. Colwell & Futuyma 1971, Vandermeer 1972). It could equally well be argued that they would not compete if they differed markedly in their choice of food or in their morphological characteristics (Lack 1971).

Previous studies

There have been many studies of niche breadth and overlap in birds generally, but very few on corvids. Olsson and Persson (1979) calculated (for late winter) overlap values for habitat, feeding technique and bill morphology among the rook, jackdaw and hooded crow, Corvus corone cornix, in Sweden. Habitat overlap was highest between the jackdaw and the hooded crow, and overall niche overlap (the average of the three component values) was highest between these two species and also between the rook and the hooded crow. Olsson and Persson's figures for habitat overlap were those computed by Loman (1980b), who also reported overlap for early winter. there was a tendency for overlap to be higher in early winter. Loman (1980b) also gave overlap values for the magpie with the other three species. These were much lower than the indices derived for the other species pairs. The values of the niche breadth indices for the four species were of the same order of magnitude in early winter. In late winter, however, there was a slight narrowing of the niche breadths of the jackdaw and magpie, a more pronounced contraction of the rook's, while the hooded crow marginally broadened its niche breadth. These data refer to two different winters and it is worth making the point that patterns of niche breadth variation within each of them were consistently different. Hogstedt (1980b), also in Sweden, reported a high degree of habitat overlap between magpies and jackdaws, having developed his line of analysis (Hogstedt 1980a) showing that competition with jackdaws had an adverse effect on magpie breeding success.

Methods and choice of indices

The data used in the calculation of niche breadth and overlap are those from the 13 months of the study for which data were available for both the rook and the carrion crow. Thus, data for September 1977, and from November 1977 to February 1978 have been excluded. This enables more meaningful comparisons to be made between the two species. The data are presented in Table 5.3 (p. 242). Also in the table is the average monthly (again over 13 months) abundance, in ha, of each resource station.

Although never utilised by foraging rooks or carrion crows, barley is included as it is biologically important to consider not only resource stations utilised by one or both species, but also those which were present and which both species avoided.

Many methods of calculating niche breadth and overlap exist. Only two for each of these niche parameters will be considered here. Linton, et al (1981) compared four of the most commonly applied measures of overlap - those of Schoener (1968), Horn (1966), Pianka (1973) and Morisita (1959). They concluded that only Schoener's gave a true indication of actual overlap over the range of potentially observable distributions, while the other indices could lead to gross errors in estimating the actual degree of overlap between species. This index was also the one favoured by Hogstedt (1980b). For these reasons Schoener's index will be considered with respect to rooks and carrion crows.

A basic desirable feature which is lacking in the measures of the above authors is a consideration of the abundance of resource states. Consider, for simplicity, three resource states, all of which are used to the same extent by a species. Now if one resource state is twice as abundant as the other two then any estimate of niche breadth which does not take this into account will be

biologically less meaningful than one which does. The same argument applies to the calculation of niche overlap between two species. Ideally, it would be even better to assess the availability of a resource to an organism, as opposed to its abundance, but in the absence of objective criteria for assessing what an animal perceives as available then abundance is the next best thing. This is made more clear if one considers that, in the present study, rooks did not forage on dung heaps, whereas they did so outside the transect area. We have no way of knowing whether rooks perceived dung heaps as being available or not within the study area. Similarly, neither species was observed utilising established barley fields in N.E. Fife, but in Aberdeenshire rooks at least certainly foraged on lodged barley (Feare et al 1974). To what extent, then, does cereal have to be lodged before rooks perceive it as being available? Such questions are not entirely empirical ones. Another aspect of this problem associated with the weighting of resource stations according to their abundance was elucidated by Hanski (1978). He stated that such weighting will be considerably complicated because resource states which occupy a large area of the total area investigated (as in this study) may not be homogeneous in the relevant dimensions. For example, prey abundance might vary (and usually does) both spatially and temporally within the same grass field (Waite 1981). Whilst these problems must not be ignored it must nevertheless make sense to attempt to impute more biological validity into the measurement of the components of the niches of organisms. Thus, a second method of computing niche overlap will be considered here, one which takes account of variation in resource abundance. This is the index developed by Hurlbert (1978).

Petraitis (1979), who also raised the problem of the perception by animals of what is an available resource, has also

developed a measure of niche overlap which takes account of the abundance of resources. It also has the property, having been derived using likelihood functions, of being statistically meaningful. The test, however, of comparing the hypothesis of no overlap with the alternative one of complete overlap is weak (Petraitis 1979), and the computation of the index unfortunately demands that all resource states be used by both species under study. Besides, as the sample sizes in the present study are so large this makes computation of the index virtually impossible (it would necessitate raising two numbers to powers > 1000 and several others to powers > 100). Petraitis´ index of overlap will not be considered here, then, although it would seem to be potentially useful with more manageable sample sizes.

The indices of niche breadth to be applied to the corvid data here are the one associated with Hurlbert´s overlap index (Hurlbert 1978), and that of Levins (1968), which does not take resource abundance into account, but is one of the most commonly used indices if not the most common. Petraitis (1979) also derived a niche breadth measure which allows for resource abundance and which, under certain circumstances, enables a statistical comparison to be made between the values obtained for different species. However, this requires that those species be from different habitats, which is not the case here.

To be specific, then, the indices to be employed in assessing the niche breadths and overlap of rooks and carrion crows are the following:

Niche breadth

$$B = 1/\sum_i p_{xi}^2 \qquad \text{(Levins 1968)}$$

$$B'_a = (AB' - a_{min})/(A - a_{min}) \qquad \text{(Hurlbert 1978)}$$

where $B' = X^2/[A\sum_i (x_i^2/a_i)]$

Niche overlap

$$D = 1 - [\sum_i (p_{xi} - p_{yi})]/2 \qquad \text{(Schoener 1968)}$$

$$L = (A/XY)\sum_i (x_i y_i/a_i) \qquad \text{(Hurlbert 1978)}$$

Notation: X - the total number of species 1 observed;

x_i - the number of individuals of species 1 observed in the ith foraging station;

p_{xi} - the proportion of individuals of species 1 observed in the ith foraging station ($= x_i/X$);

Y - the total number of species 2 observed;

y_i - the number of individuals of species 2 observed in the ith foraging station;

p_{yi} - the proportion of individuals of species 2 observed in the ith foraging station ($= y_i/Y$);

A - the total resource abundance;

a_i - the abundance of the ith foraging station;

a_{min} - the abundance of the least abundant resource station.

B ranges from 1 to N, where N is the number of different types of resource station. High values indicate broad niches. A value of N would mean that the species used all resource stations to an equal extent.

B'_a takes values ranging from 0 to 1 and measures ".....the degree to which intraspecific encounters have been minimised as a result of the species utilizing or tending to utilize all available resource states in proportion to their abundances." (Hurlbert 1978). A value of 0 would indicate that the species was a specialist, and a value of 1 a generalist.

D also takes values from 0 to 1, signifying no overlap to complete overlap respectively.

L ranges from 0 through 1 to higher values. A value of 0 indicates that the two species have utilized no resource states in common. A value of 1 indicates that both species utilise all resource states in direct proportion to their abundances, and values > 1 mean that both species tend to use the same resource states to a disproportionately high degree.

Results

The values obtained for niche breadth and overlap of rooks and carrion crows were thus:

	Rook		Crow
B	2.30		3.98
B'_a	0.62		0.33
D		0.72	
L		1.58	

As can be seen Levins' method of computing niche breadth resulted in a higher value for the crow, whereas Hurlbert's method resulted in the rook ostensibly having a broader niche. The two overlap indices used show that the two species used the same field types to a large extent.

Discussion

The values obtained for the niche breadth indices conflicted in that one method pointed to the rook as being more of a generalist (Hurlbert's index), while the other suggested that the carrion crow was more of a generalist in the range of habitats it utilised (Levins' index). This illustrates the effect of including resource abundances in the assessment of niche breadth. The carrion crow tended to use resources more evenly than the rook (evidenced by Levins index values) but this only means that it must have been specialising to some degree. This is because there were marked differences in the abundances of the resources present. Hurlbert's index probably gives a truer indication of actual niche breadth as resource abundances are taken into account. If one accepts the values of Hurlbert's index as being truer reflections of niche breadth then the result (that rooks are more generalist in their habitat preferences than carrion crows) is complemented by studies which show that the rook takes a greater variety of food types than the carrion crow (e.g. Lockie 1956b, but bear in mind that abundances

of different prey types was not considered in that study). Loman (1980b) also found, over the whole winter, that the rook has a broader niche than the hooded crow).

Niche overlap between the two species in this study was high, although not as high as that between the rook and hooded crow in Sweden (Loman 1980b). Throughout the year in Fife Schoener's (1968) index gave a value of 0.72 compared to the 0.83 and 0.91 in early and late winter respectively computed by Loman. Loman's study, however, was confined to grass habitats and did not consider other foraging stations, so the values obtained may overestimate the real degree of overlap between these two species. It is also possible that the hooded crow and the carrion crow have different habitat requirements, or that the overall environmental characteristics are so different between Fife and south Sweden as to produce differences in overlap. However, the Fife figures refer to all seasons whereas Loman's only refer to winter. Comparisons of niche breadth and overlap throughout the year in Fife are reported below.

Hurlbert's (1978) index again shows that the rook and carrion crow overlap to a high degree, but also that both species were foraging on some of the (same) field types more intensively than would be expected from their abundances. From Tables 5.1 and 5.2 (pp. 230-235 and 236-241) it can be seen that these were mainly grass, stubble and dung.

The high values obtained here for feeding habitat overlap do not mean, of course, that both species were taking the same types of food on the same field types, and therefore that they were competing (passively). The degree of competition, if any, between them cannot be gauged, though, as differences in the times at which both species were feeding on the same field were not taken into account. Such differences could mean that different prey items (or

size classes of the same prey) were being taken by the two species. The same might be true of different fields but of the same type. Nevertheless, rooks and carrion crows were seen on many occasions feeding on the same field at the same time, so competition probably was taking place. The fact that high qualitative degrees of diet overlap exist between them (e.g. Lockie 1956b, Holyoak 1968) tends to support this. Throughout this whole study only one agonistic interaction over food was observed between a rook and a carrion crow. A possible reason why there might be low levels of active competition between these corvids is discussed in chapter 7.

TEST OF SOME HYPOTHESES REGARDING NICHE BREADTH AND OVERLAP

MacArthur & Pianka (1966) suggested that an optimally foraging predator should narrow its utilisation of food patches (i.e. its niche breadth) when food density is high. Loman (1980b) found that, in fact, corvids generally tended to narrow their niche breadth when food became scarcer, thus failing to confirm MacArthur & Pianka´s hypothesis. As corvids do not pursue their prey, Loman stated, then this was not surprising as MacArthur & Pianka´s model referred to predators which are "pursuers". However, "pursuit time" in the model included not only pursuit, but also capture and eating time. Thus the hypothesis technically refers to any animal which has a significant prey handling time, not only one which pursues its prey. Loman (1980b) indeed did report that in one winter the hooded crow and the magpie broadened their niches when food became scarcer. MacArthur & Pianka´s (1966) hypothesis that the niche breadths of species become narrower when food is not scarce will be re-investigated here. The rook probably spends more time capturing and handling its prey than does the carrion crow, as evidenced by the

greater numbers of earthworms and leatherjackets taken by rooks, and the probing and digging movements associated with capturing them (Lockie 1956b). Although carrion crows might spend more time pursuing and handling small mammalian prey this will be offset by reductions in such times when feeding on carrion. If, then, the rook is generally more of a "pursuer" than the carrion crow it follows from MacArthur & Pianka's model that rooks should show more niche breadth reduction than carrion crows when food density is high. This will be investigated here.

MacArthur & Pianka (1966) also postulated that when faced with competition from other species then a species should show a narrowing of its utilised habitat spectrum. Hogstedt (1980a) reported close agreement between competition and niche overlap in magpies and jackdaws. Therefore, if a high degree of overlap between rooks and carrion crows does mean that they are competing with one another, then according to this formulation the niche breadths of the two should be smaller than when overlap between them is less. There is already some suggestive evidence that rooks restricted their habitat preferences perhaps in order to avoid active competition with carrion crows (see earlier section on discussion of the simple index of habitat preferences). As there probably was some degree of passive competition between rooks and carrion crows in this study, the relationship between niche overlap and the niche breadths of the two species for each month of the study will also be scrutinised.

To recap, the following hypotheses will be tested:

1. When food is not scarce then the niche breadths of rooks and carrion crows will be smaller and that

2. any reduction in their niche breadths will be greater for the rook.

3. There will be a negative correlation between monthly habitat

overlap of the two species and the respective monthly niche breadths of each of them.

Methods

The indices of niche breadth and overlap used above will again be used here. For comparative purposes the standardised form of Levins' (1968) index of niche breadth will be used. This is simply the index as derived using the formula above divided by the appropriate number of resource stations used in its computation. This results in values between 0 and 1.

As mentioned in chapter 4 no estimate of food abundance was made in this study which makes the testing of hypothesis 1 difficult. There was strong circumstantial evidence, though, that a time of food shortage for rooks was in the summer, as it was further north along the coast in Aberdeenshire (Feare et al 1974). With carrion crows the suspected times of food shortage included spring and late winter. For the purposes of testing hypotheses 1 and 2, then, the months of food shortage for the rook were taken as July and August 1978, and for the carrion crow March 1978 and January and February 1979. These months for the carrion crow correspond roughly to Loman's (1980b) period of late winter - also when food availability was low.

In testing hypothesis 3 niche overlap and breadths were computed for each of the months for which carrion crow and rook data were available (13 in all). Spearman's rank correlation tests (Siegel 1956) were then applied, comparing overlap values with breadth values for each species. To make comparisons meaningful the indices of Levins and Schoener, which do not take resource abundance into account, were compared with each other, while Hurlbert's indices, which do account for resource abundance were compared with one another. All tests used were one-way ones.

Results

Table 5.4 (p. 243) shows the values of the niche breadth indices with respect to hypotheses 1 and 2. Levins' index suggested that rook niche breadth narrowed when food became scarce, whereas Hurlbert's index suggested the opposite. Similarly, carrion crow niche breadth widened when food became scarce according to Levins' index, while Hurlbert's index indicated that it narrowed. Therefore, no clear pattern emerged from the data regarding the relationship between food availability and niche breadth.

Table 5.5 (p. 244) shows the values of the various indices for each species for each month of the study. The results of Spearman rank correlation tests of hypothesis 3 were as follows:

Rook niche breadth (B)/niche overlap (D): $r= -0.09$, $N=13$, $p> 0.05$

Carrion crow niche breadth (B)/niche overlap (D): $r= -0.52$, $N=13$, $p< 0.05$

Rook niche breadth (B'_a)/niche overlap (L): $r= -0.41$, $N=13$, $p> 0.05$

Carrion crow niche breadth (B'_a)/niche overlap (L)= $r= -0.23$, $N=13$, $p>0.05$

While both species narrowed their niche breadth when overlap was high only the carrion crow did so to a statistically significant degree, and only when Levins' and Schoener's indices were compared.

Discussion

No unequivocal relationship was found between the niche breadths of rooks or carrion crows at their respective times of food shortage and at other times of the year. However, the data do suggest that respective niche sizes of both species were not

different at these two times. This means, then, that hypothesis 1 was not confirmed, and neither was hypothesis 2. Possible explanations of why niche breadth did not differ at times of food scarcity and other times include the possibility that during the presumed periods of food scarcity food was, in fact, not scarce. Loman (1980b), however, also failed to find a consistent widening of the niche breadth of the hooded crow from early to late winter (i.e. from moderate to low food availability). Although the rook actually restricted its niche size in his study from early to late winter the evidence that late winter was a time of food scarcity for rooks was weak. Indeed, there was a suggestion that rooks more than hooded crows preferred "intermediate" habitats (i.e. those meadows which were classified as being in between "dry" and "moist" ones), and that the biomass of available invertebrates in them was at its lowest during July. Unfortunately Loman did not measure corvid niche breadths (or overlap) in the summer. So there is no evidence to support hypothesis 1 either in the present study or in Loman´s. Loman rationalised this by stressing that MacArthur & Pianka´s (1966) model referred to birds which had high prey pursuit and handling times, which corvids did not have. As pointed out earlier, and as formed the basis for hypothesis 2, corvids do spend some time pursuing and handling at least some of their prey. So why don´t rooks and carrion crows show a restriction of their niche breadths when food is not scarce? Clearly the realised niche breadth of any species will be dependent on what habitats are available. This availability will in turn depend not only on the presence of habitats in the environment but also on whether, and to what degree, they are being used by other species. Thus Ulfstrand (1967) in a study of a community composed of several tits, Parus spp., and other, ecologically similar small passerines, found that some species´ niche

breadths remained constant throughout the year (e.g. treecreeper Certhia familiaris and goldcrest Regulus regulus), while those of other species (e.g. coal tit Parus ater and willow tit P. montanus) fluctuated markedly and at different times of the year irrespective of food abundance. Complicated relationships between niche breadth and overlap existed among these birds due to the interdependence of how each was using its habitat.

Relationships with other species are likely, then, to be more important in determining niche size and overlap of species than is food availability per se. The finding that hypothesis 3 was in large measure confirmed supports this interpretation. The niche breadths of rooks and carrion crows were inversely correlated, in one test significantly so for the carrion crow, with overlap between them. Morse (1974) postulated that if two species overlap in their use of resources then the species which is socially dominant should show the lesser change in pattern of resource use. In the case of rooks and carrion crows in Fife this should mean that the rook, being subordinate to the carrion crow (see chapter 7), should show the greater change in resource use when overlap is high. Habitats which could have been used by both species but were not because they were not present in the study area or just outside it were few in number. That is, both species were occupying a range of habitats approximating to their realised niches. Any change in resource use by rooks, then, should have been evidenced by a restriction of their niche breadth. Contrary to this prediction, carrion crows showed the greater niche breadth restriction when overlap was high. Morse (1974) pointed out, though, that if the dominant species would have to expend much valuable energy in preventing the subordinate species from using resources, and is rarer than the subordinate species, then it might be advantageous for it to change its pattern of resource

use. This seems to be the case in this study. Despite being dominant to the rook the carrion crow would have great difficulty in expelling large flocks of rooks from its territory. Morse (1974) stated that this pattern was rare and of lesser importance than the case where the subordinate species restricts its niche breadth to a greater extent than the dominant species. He quoted only one other instance of it - a study by Stoecker (1972) on niche breadth variation in voles Microtus spp. Loman's (1980b) data, as they bear on this question, tended to show the usual pattern of a greater restriction in the niche breadth of subordinate species (rook, jackdaw, magpie) than the dominant species (hooded crow). The strength of this relationship appeared weak, but in any case hooded crows in his study were found in larger groups than carrion crows in the present study and, more significantly, rooks were observed to be in much smaller groups than in Fife (mean size of 5.9 individuals compared to 16.75 at the same time of year). The phenomenon of the dominant species possibly avoiding the subordinate by showing a greater narrowing of its niche breadth in potentially competitive situations could be more widespread and would seem to be most applicable to pairs of species of which the subordinate one was highly sociable and able to effectively increase its competitive ability as a result of receiving less overt aggressive attention from solitary competitors. More research on other species into this area could be rewarding. Chapter 7 considers the competitive abilities of rooks and carrion crows in more detail.

Table 5.1. The availability of each field type expressed as a percentage of the total transect area (%A) and the proportion of foraging rooks (%R) doing so on each of these field types in each month of the study. The index of utilisation, based on Dunnet & Patterson (1968), is %R divided by %A.

		1977				1978	
		Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
GRASS	%A	61.41	61.41	61.41	64.70	64.70	64.70
	%R	51.94	55.56	42.50	58.38	37.07	12.10
	Index	0.85	0.90	0.69	0.90	0.57	0.19
STUBBLE	%A	21.88	21.88	15.14	15.14	15.14	11.83
	%R	43.70	34.32	13.94	2.70	47.20	72.42
	Index	2.00	1.57	0.92	0.18	3.12	6.12
PLOUGH	%A	0.82	4.53	11.00	11.68	11.68	11.68
	%R	3.41	9.45	15.68	28.11	11.85	8.13
	Index	4.16	2.09	1.43	2.41	1.01	0.70
SOWN BARLEY	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-
BRAIRD	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-
DUNG	%A	0	0	0	0	0	3.30
	%R	0	0	0	0	0	7.34
	Index	-	-	-	-	-	2.22
WASTE	%A	2.68	2.68	2.68	2.68	2.68	2.68
	%R	0.08	0.27	0	10.81	3.88	0
	Index	0.03	0.10	0	4.03	1.45	0
POTATOES	%A	4.12	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	0	-	-	-	-	-
SOWN POTATOES	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-

Table 5.1 (continued)

		1977				1978	
		Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
FALLOW	%A	3.30	3.30	0	0	0	0
	%R	0.67	0.36	0	0	0	0
	Index	0.20	0.11	-	-	-	-
SOWN GRASS	%A	0	0	3.30	0	0	0
	%R	0	0	27.87	0	0	0
	Index	-	-	8.45	-	-	-
PLOUGH IN PROGRESS	%A	0	0.41	0.67	0	0	0
	%R	0	0	0	0	0	0
	Index	-	0	0	-	-	-
BARLEY	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-
MUD	%A	5.66	5.66	5.66	5.66	5.66	5.66
	%R	0	0	0	0	0	0
	Index	0	0	0	0	0	0

Table 5.1 (continued)

1978

		Mar.	Apr.	May	Jun.	Jul.	Aug.
GRASS	%A	64.70	64.70	64.70	64.70	64.86	65.53
	%R	36.80	21.07	64.73	96.12	99.74	85.86
	Index	0.57	0.33	1.00	1.49	1.54	1.31
STUBBLE	%A	0	0	0	0	0	5.44
	%R	1.97	0	0	0	0	9.28
	Index	-	-	-	-	-	1.71
PLOUGH	%A	10.78	5.06	2.52	0	0.67	0
	%R	0	0	0	0	0	1.47
	Index	0	0	0	-	0	-
SOWN BARLEY	%A	9.22	21.76	1.66	0	0	0
	%R	58.71	59.55	15.83	0	0	0
	Index	6.37	2.74	9.54	-	-	-
BRAIRD	%A	0	0	20.10	2.72	0	0
	%R	0	0	11.62	0.09	0	0
	Index	-	-	0.58	0.03	-	-
DUNG	%A	4.97	0	0	0.10	0.10	0.10
	%R	2.53	0	0	0	0	0
	Index	0.51	-	-	0	0	0
WASTE	%A	2.68	2.68	2.68	2.68	2.68	2.68
	%R	0	2.81	0.40	0.27	0.13	3.38
	Index	0	1.05	0.15	0.10	0.05	1.26
POTATOES	%A	0	0	0	2.12	4.23	4.23
	%R	0	0	0	3.43	0	0
	Index	-	-	-	1.62	0	0
SOWN POTATOES	%A	0	0	2.12	2.12	0	0
	%R	0	0	2.10	0	0	0
	Index	-	-	0.99	0	-	-

Table 5.1 (continued)

		1978					
		Mar.	Apr.	May	Jun.	Jul.	Aug.
FALLOW	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-
SOWN GRASS	%A	0	0	0	0.82	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	0	-	-
PLOUGH IN PROGRESS	%A	1.84	0	0.42	0	0	0
	%R	0	16.57	5.31	0	0	0
	Index	0	-	12.64	-	-	-
BARLEY	%A	0	0	0	19.04	21.76	16.32
	%R	0	0	0	0	0	0
	Index	-	-	-	0	0	0
MUD	%A	5.66	5.66	5.66	5.66	5.66	5.66
	%R	0	0	0	0	0	0
	Index	0	0	0	0	0	0

Table 5.1 (continued)

		1978				1979	
		Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
GRASS	%A	65.53	65.53	64.92	64.32	64.32	64.32
	%R	26.17	34.76	83.13	64.84	48.64	75.23
	Index	0.40	0.53	1.28	1.01	0.76	1.17
STUBBLE	%A	21.76	21.76	7.24	3.52	1.76	0
	%R	71.03	61.61	9.05	0	0	0
	Index	3.26	2.83	1.25	0	0	-
PLOUGH	%A	0.91	3.17	17.41	23.56	23.68	23.68
	%R	0.23	0	7.82	33.63	0.27	4.66
	Index	0.25	0	0.45	1.43	0.01	0.20
SOWN BARLEY	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-
BRAIRD	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-
DUNG	%A	0.10	0	0	0	1.76	3.52
	%R	0	0	0	0	51.09	20.11
	Index	0	-	-	-	29.03	5.71
WASTE	%A	2.68	2.68	2.68	2.68	2.68	2.68
	%R	0.58	2.09	0	0	0	0
	Index	0.22	0.78	0	0	0	0
POTATOES	%A	3.17	0.91	0	0	0	0
	%R	1.99	1.13	0	0	0	0
	Index	0.63	1.24	-	-	-	-
SOWN POTATOES	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-

Table 5.1 (continued)

		1978				1979	
		Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
FALLOW	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-
SOWN GRASS	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-
PLOUGH IN PROGRESS	%A	0.15	0.15	1.95	0.12	0	0
	%R	0	0.40	0	1.54	0	0
	Index	0	2.67	0	12.83	-	-
BARLEY	%A	0	0	0	0	0	0
	%R	0	0	0	0	0	0
	Index	-	-	-	-	-	-
MUD	%A	5.66	5.66	5.66	5.66	5.66	5.66
	%R	0	0	0	0	0	0
	Index	0	0	0	0	0	0

Table 5.2. The availability of each field type expressed as a percentage of the total transect area (%A) and the proportion of foraging carrion crows (%C) doing so on each of these field types in each month of the study. The index of utilisation, based on Dunnet & Patterson (1968), is %C divided by %A.

		1977				1978	
		Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
GRASS	%A	61.41	61.41	61.41	64.70	64.70	64.70
	%C	-	12.64	-	-	-	-
	Index	-	0.21	-	-	-	-
STUBBLE	%A	21.88	21.88	15.14	15.14	15.14	11.83
	%C	-	82.76	-	-	-	-
	Index	-	3.78	-	-	-	-
PLOUGH *	%A	0.82	4.53	11.00	11.68	11.68	11.68
	%C	-	4.60	-	-	-	-
	Index	-	1.02	-	-	-	-
SOWN BARLEY	%A	0	0	0	0	0	0
	%C	-	0	-	-	-	-
	Index	-	-	-	-	-	-
BRAIRD	%A	0	0	0	0	0	0
	%C	-	0	-	-	-	-
	Index	-	-	-	-	-	-
DUNG	%A	0	0	0	0	0	3.30
	%C	-	0	-	-	-	-
	Index	-	-	-	-	-	-
WASTE	%A	2.68	2.68	2.68	2.68	2.68	2.68
	%C	-	0	-	-	-	-
	Index	-	0	-	-	-	-
POTATOES	%A	4.12	0	0	0	0	0
	%C	-	0	-	-	-	-
	Index	-	-	-	-	-	-
SOWN POTATOES	%A	0	0	0	0	0	0
	%C	-	0	-	-	-	-
	Index	-	-	-	-	-	-

Table 5.2 (continued)

		1977				1978	
		Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
FALLOW	%A	3.30	3.30	0	0	0	0
	%C	-	0	-	-	-	-
	Index	-	0	-	-	-	-
SOWN GRASS	%A	0	0	3.30	0	0	0
	%C	-	0	-	-	-	-
	Index	-	-	-	-	-	-
PLOUGH IN PROGRESS	%A	0	0.41	0.67	0	0	0
	%C	-	0	-	-	-	-
	Index	-	0	-	-	-	-
BARLEY	%A	0	0	0	0	0	0
	%C	-	0	-	-	-	-
	Index	-	-	-	-	-	-
MUD	%A	5.66	5.66	5.66	5.66	5.66	5.66
	%C	-	0	-	-	-	-
	Index	-	0	-	-	-	-

Data are not available for September 1977 or November 1977 to February 1978 inclusive.

Table 5.2 (continued)

1978

		Mar.	Apr.	May	Jun.	Jul.	Aug.
GRASS	%A	64.70	64.70	64.70	64.70	64.86	65.53
	%C	13.21	27.27	57.53	51.85	74.42	89.66
	Index	0.20	0.42	0.89	0.80	1.15	1.37
STUBBLE	%A	0	0	0	0	0	5.44
	%C	0	0	0	0	0	0
	Index	-	-	-	-	-	0
PLOUGH	%A	10.78	5.06	2.52	0	0.67	0
	%C	5.48	0	0	0	4.65	0
	Index	0.51	0	0	-	6.94	-
SOWN BARLEY	%A	9.22	21.76	1.66	0	0	0
	%C	39.62	71.60	0	0	0	0
	Index	4.30	3.29	0	-	-	-
BRAIRD	%A	0	0	20.10	2.72	0	0
	%C	0	0	30.14	0	0	0
	Index	-	-	1.50	0	-	-
DUNG	%A	4.97	0	0	0.10	0.10	0.10
	%C	47.17	0	0	27.78	4.65	1.72
	Index	9.49	-	-	277.80	46.50	17.20
WASTE	%A	2.68	2.68	2.68	2.68	2.68	2.68
	%C	0	0	0	0	6.98	6.90
	Index	0	0	0	0	2.60	2.57
POTATOES	%A	0	0	0	2.12	4.23	4.23
	%C	0	0	0	0	0	0
	Index	-	-	-	0	0	0
SOWN POTATOES	%A	0	0	2.12	2.12	0	0
	%C	0	0	2.74	3.70	0	0
	Index	-	-	1.29	1.75	-	-

Table 5.2 (continued)

		1978					
		Mar.	Apr.	May	Jun.	Jul.	Aug.
FALLOW	%A	0	0	0	0	0	0
	%C	0	0	0	0	0	0
	Index	-	-	-	-	-	-
SOWN GRASS	%A	0	0	0	0.82	0	0
	%C	0	0	0	12.96	0	0
	Index	-	-	-	15.80	-	-
PLOUGH IN PROGRESS	%A	1.84	0	0.42	0	0	0
	%C	0	0	0	0	0	0
	Index	0	-	0	-	-	-
BARLEY	%A	0	0	0	19.04	21.76	16.32
	%C	0	0	0	0	0	0
	Index	-	-	-	0	0	0
MUD	%A	5.66	5.66	5.66	5.66	5.66	5.66
	%C	0	1.14	1.37	1.85	6.98	1.72
	Index	0	0.20	0.24	0.33	1.23	0.30

Table 5.2 (continued)

		1978				1979	
		Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
GRASS	%A	65.53	65.53	64.92	64.32	64.32	64.32
	%C	47.06	58.62	68.97	33.33	55.00	24.14
	Index	0.72	0.89	1.06	0.52	0.86	0.38
STUBBLE	%A	21.76	21.76	7.24	3.52	1.76	0
	%C	4.41	6.90	0	33.33	0	0
	Index	0.20	0.32	0	9.47	0	-
PLOUGH	%A	0.91	3.17	17.41	23.56	23.68	23.68
	%C	0	0	20.69	16.67	5.00	13.79
	Index	0	0	1.19	0.71	0.21	0.58
SOWN BARLEY	%A	0	0	0	0	0	0
	%C	0	0	0	0	0	0
	Index	-	-	-	-	-	-
BRAIRD	%A	0	0	0	0	0	0
	%C	0	0	0	0	0	0
	Index	-	-	-	-	-	-
DUNG	%A	0.10	0	0	0	1.76	3.52
	%C	1.47	0	0	0	25.00	55.17
	Index	14.70	-	-	-	14.20	15.67
WASTE	%A	2.68	2.68	2.68	2.68	2.68	2.68
	%C	7.35	17.24	10.34	0	15.00	0
	Index	2.74	6.43	3.86	0	5.60	0
POTATOES	%A	3.17	0.91	0	0	0	0
	%C	2.94	0	0	0	0	0
	Index	0.93	0	-	-	-	-
SOWN POTATOES	%A	0	0	0	0	0	0
	%C	0	0	0	0	0	0
	Index	-	-	-	-	-	-

Table 5.2 (continued)

		1978				1979	
		Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
FALLOW	%A	0	0	0	0	0	0
	%C	0	0	0	0	0	0
	Index	-	-	-	-	-	-
SOWN GRASS	%A	0	0	0	0	0	0
	%C	0	0	0	0	0	0
	Index	-	-	-	-	-	-
PLOUGH IN PROGRESS	%A	0.15	0.15	1.95	0.12	0	0
	%C	0	0	0	0	0	0
	Index	0	0	0	0	-	-
BARLEY	%A	0	0	0	0	0	0
	%C	0	0	0	0	0	0
	Index	-	-	-	-	-	-
MUD	%A	5.66	5.66	5.66	5.66	5.66	5.66
	%C	36.76	17.24	0	16.67	0	6.90
	Index	6.49	3.05	0	2.95	0	1.22

Table 5.3. The average monthly abundance of each crop type (in ha) and the respective numbers of rooks and carrion crows observed foraging on them. These figures only refer to the 13 months of the study for which carrion crow data are available, and are those used in calculating indices of niche breadth and overlap.

	No. of rooks	No. of crows	Abundance
GRASS	6603	285	170.90
PLOUGH	449	22	23.61
STUBBLE	2249	79	16.97
MUD	0	40	14.98
BARLEY	0	0	11.63
WASTE	78	23	7.09
SOWN BARLEY	579	84	6.64
BRAIRD	117	22	4.65
POTATOES	69	2	2.98
DUNG	348	65	2.19
PLOUGH IN PROGRESS	124	0	1.03
SOWN POTATOES	21	4	0.86
FALLOW	8	0	0.67
TREES	0	3	0.38
SOWN GRASS	0	7	0.17
STACKS	2	0	0.10
ANIMAL FEEDING TROUGH	0	1	0.01
SHEEP BACK	1	0	0.01
TOTALS	10648	637	264.87

Table 5.4. Niche breadths of rooks and carrion crows at times when food was presumed to be in short supply and at all other times. The values in parentheses are those derived when data from all months of the study were included, and not just those for when carrion crow data was available (i.e. 16 as opposed to 11 months). Values of Levins' breadth index (B) have been standardised (see text). Times of food shortage for rooks were July and August 1978, and for carrion crows March 1978 and January and February 1979.

		Time of food shortage	Other times
Rook	B	0.10	0.14 (0.15)
	B_a	0.70	0.60 (0.62)
Crow	B	0.36	0.20
	B_a	0.13	0.19

Table 5.5. Niche breadth and overlap values for rooks and carrion crows in each month of the study. Values of Levins' breadth index (B) have been standardised (see text).

	B_{rook}	B_{crow}	D	$B'_{a\,rook}$	$B'_{a\,crow}$	L
October 1977	.256	.158	.52	.80	.31	1.51
March 1978	.259	.315	.57	.29	.17	2.66
April 1978	.390	.283	.81	.31	.40	2.05
May 1978	.241	.260	.71	.34	.61	0.78
June 1978	.108	.274	.52	.67	.004	0.77
July 1978	.144	.251	.75	.65	.005	1.15
August 1978	.191	.177	.89	.74	.45	1.26
September 1978	.218	.343	.33	.41	.28	0.37
October 1978	.250	.306	.44	.51	.46	0.64
November 1978	.203	.270	.77	.82	.72	0.98
December 1978	.267	.514	.50	.75	.25	0.57
January 1979	.287	.366	.74	.06	.20	7.68
February 1979	.273	.432	.49	.49	.11	3.47

Chapter 6. The diet of young rooks

INTRODUCTION

There have been several published reports of rook diet, some of which were referred to in chapter 4. One of the earliest was that by Newstead (1908) whose analysis of 14 gizzards of mainly young birds revealed moth larvae (Noctuidae) and beetles (Coleoptera) to be the commonest animal prey, while potato and wheat were common components of the birds' vegetable diet. Collinge (1910, 1920, 1927) found 71% and 29% of the rook's food to be composed of vegetable (mainly grain) and animal items respectively (over 800 gizzards examined), and 59% and 41% respectively by volume (over 1300 gizzards). The most common invertebrate prey were beetles and earthworms, and wheat was the most common cereal recorded. Campbell (1936) analysed the gizzards of 68 young rooks. The food contents comprised vegetable food (87.9%), mainly cereals (60.4%), invertebrates (11.5%), mostly insects and larvae (10.7%) and vertebrate remains (0.6%). Lockie (1955, 1959) used a different method to investigate the diet of young rooks. He prevented the passage of food into the gizzard by attaching wire collars around the necks of nestlings. He found that the greatest volume of food fed to the nestlings consisted of earthworms of various species. Lesser amounts of grain and other invertebrates (notably lepidopterous larvae) were recorded, but there was much variation in the contents of nestling gullets both between different rookeries and also between the same rookeries in different years. Lockie (1956b) also analysed 73 rook gizzards. Over half of these at all times of the year contained earthworm remains, while Coleoptera were present in at least some gizzards at all times. Over 80% of gizzards contained grain throughout the year and at some times all of them did so.

Holyoak (1968) analysed 191 gizzards and summarised Lockie's (1956b) results with his own. Again, most birds had fed on grain in all months of the year. Slugs and snails, earthworms, lepidopterous larvae and pupae and beetles also featured in the diet at all times. Holyoak (1972) reported analyses of 933 gizzards collected during 1944/45 for the Ministry of Agriculture Investigation into rook habits (Fisher 1948). Considerable amounts of cereal were recorded and large proportions of birds had eaten beetles in all months. In summer, leatherjackets, Lepidoptera, spiders and Hymenoptera were each present in about a fifth of the gizzards.

The results of gizzard analyses in other countries are similar to those from Britain. Most of Fog's (1963) 670 Danish rook gizzards contained both animal and vegetable matter, barley being the most common vegetable food. Earthworms, beetles and flies (Diptera) were the main invertebrate prey. Feijen (1976) reported grain to be the most common food of rooks in the Netherlands, again with beetles, lepidopterous larvae and leatherjackets important invertebrate prey. Gromadska (1980) estimated the rook's diet to consist of slightly more animal than vegetable material. Once again large amounts of grain and beetles were recorded. In New Zealand, Porter (1979) noted greater volumes of invertebrate prey (particularly earthworms, beetles and Diptera) and cereals seemed to be a less important, but nevertheless plentiful, component of diet than in Britain and Europe. The consensus from these studies is that grain is a significant food source for rooks when it is available, as also is a wide variety of invertebrates, but notably earthworms, leatherjackets and beetles (see recent resume of published studies by Jablonski 1979). Observations in the wild and in captivity have confirmed that rooks prefer these foods (Feare et al 1974, Purchas 1980).

This chapter presents the results of an investigation of

the diet of nestling rooks at one rookery in the study area.

METHODS

Twenty rook nestlings were found dead on 10 May 1977 on the ground below rookery 50/07 (West Lodge, Balcaskie). They had been shot and were estimated to have been dead for about a day. The remiges and rectrices of most of them were well grown and these birds were probably "branchers", but some may still have been in the nest when shot, being ejected from the nest by the parent birds. None of the corpses hosted any obvious ectoparasites.

Each nestling was weighed on the day of finding and collecting them and the following measurements were also taken: weight; wing length (maximum chord); bill depth (at the middle of the nostril); and bill length (from the tip of the upper mandible to the base of the skull). Descriptions of these methods may be found in Svensson (1975). The gizzard of each nestling was then removed and emptied of its contents. These were preserved in 70% alcohol to await analysis.

The contents of each gizzard were sorted in water into animal remains, vegetable matter and stones and grit. This was done in two stages, the first, preliminary sorting by eye and the second using a 2.5x-10x binocular microscope. The gizzard contents were then dried in a slow oven and weighed. All remains were then identified as accurately as possible and the volumes of animal, vegetable and mineral matter measured, by displacement in water, to the nearest 0.25 cm^3. Care was taken to gently compress the material to expel all air bubbles when measuring the volumes.

RESULTS

Identification of invertebrate remains was assisted by Britton (1956), Chinery (1973), Crowson (1956) and Lindroth (1974). Spiders were identified by their legs usually, but the epigyne of a female spider was found in one gizzard. Bird lice and thrips were found whole. The elytra of beetles were usually fragmented. Identification of this group to family level usually rested on the discovery of head parts and occasionally on the structure of any legs present. All but one beetle larvae were broken and probably more than half digested. Caterpillars were found partly digested but still whole. Adult crane fly bodies were whole, one with a wing still attached. Leatherjackets were also found whole and some were more or less intact, as were maggots. The inclusion of adult flies in the diet was indicated by undigested heads and legs. Table 6.1 (p. 254) shows which food items were recorded in each gizzard.

All gizzards contained vegetable material, predominantly barley while only two did not contain any invertebrate remains and only one did not contain any stones or grit. Shells have been recorded here only when one or more snail shell apices were found in the gizzard. The presence of a shell apex is perhaps indicative of the likelihood that snails were taken deliberately as food whereas if shell fragments only were present then they could have been taken incidentally with other food items.

Table 6.2 (p. 255) shows the dry weights of the different sorts of material found in each gizzard. The fullest gizzard contained matter weighing 6.975 g while the constituents of the emptiest weighed 0.069 g. In Table 6.3 (p. 256) the respective volumes of vegetable, animal and mineral contents of gizzards are shown. The total maximum volume was 6.25 cc and the least was 0.50 cc.

The measurements taken of the nestlings are shown in Table 6.4 (p. 257). One nestling was wet and so was not weighed. The bill of another had been mutilated and was not measured. The mean weight of the nestlings was 422.47 g (s.d. = 65.63, N = 19). The mean wing length was 211.20 mm (s.d. = 33.39, N = 20). The mean bill length and mean bill depth were 51.25 mm and 14.35 mm respectively (s.d.'s = 3.99 and 1.40, N = 19 in both cases). All of these measurements were significantly correlated with each other. Here is the matrix showing the correlation coefficients for each pair:

	Weight	Wing length	Bill length	Bill depth
Weight	1.000	0.476[1]	0.747[2]	0.681[3]
Wing length		1.000	0.834[4]	0.550[5]
Bill length			1.000	0.630[6]
Bill depth				1.000

[1] 17 df, $p < 0.05$ [2] 16 df, $p < 0.001$ [3] 16 df, $p < 0.01$
[4] 17 df, $p < 0.001$ [5] 17 df, $p < 0.02$ [6] 17 df, $p < 0.01$

There was a significant positive correlation between the weight of a nestling and the weight of vegetable matter contained in its gizzard ($r = 0.656$, 17 df, $p < 0.01$) and a significant negative correlation between nestling wing length and weight of stones and grit in the gizzard ($r = -0.478$, 18 df, $p < 0.05$). There were no other significant correlations between the various measures of nestling size and gizzard content weights. Similarly, there was a significant positive correlation between nestling weight and the volume of vegetable matter in the gizzard ($r = 0.574$, 17 df, $p < 0.02$) and a significant negative correlation between nestling wing length and volume of mineral matter in the gizzard ($r = -0.465$, 18

df, $p < 0.05$).

DISCUSSION

The food items recorded in this study represent a sample of those recorded in other investigations, agreeing well with studies of nestling diet (Lockie 1955), and also of adult diet in the month of May (Campbell 1936, Lockie 1956b, Holyoak 1968, 1972). The bird louse discovered in one gizzard was probably ingested fortuitously. Similarly, the single thrip recorded was most likely to have been fed to the nestling incidentally with other material. Thrips are certainly too small on which to prey. As with Holyoak's (1968, 1972) reports, ground beetles were an important component of the Coleopteran part of the diet. But compared to previous studies of rook diet the variety of foods recorded here is notable because of the absence of earthworms. Despite a thorough search for earthworm chaetae and gizzard rings none were found. Holyoak (1972) mentioned the problem of the quick digestion of earthworms and other invertebrates, and in controlled conditions van Koersveld (1951) found that digestion of earthworms by jackdaws and hooded crows was quite advanced only 20 minutes after ingestion, while all traces of them had disappeared three days after their ingestion followed by immediate sacrifice of the birds. Luniak (1977) found that no traces of earthworms remained in rook gizzards only 30-40 minutes after ingestion, but that little digestion took place in the same amount of time if the birds were killed shortly after ingestion. The young rooks in the present study had probably been dead long enough for complete digestion of earthworms to occur, even allowing for the slower digestion after death. Whether these birds had in fact been fed earthworms remains unknown, but the complete absence of chaetae suggests that they had not. Many soft bodied invertebrates,

especially insect larvae, could have been fed to them but were not recorded because they had been completely digested. The remains of adult beetles were certainly well digested and most of them consisted of the very fragmented hard elytra. This suggests that digestion may have been too far advanced to leave traces of larvae, and possibly other invertebrates also. Beetle orders other than the ones noted in Table 6.1 (p. 254) may also have been represented in the diet.

Much of the barley grain recorded had also been well digested although there were many undigested whole grains in the gizzards. These latter were invariably damaged at one end, signifying that they had sprouted. Some still had the beginnings of a root system attached. This shows clearly that the grain which was fed to these young birds had been dug or pulled up from sown barley fields, and it may have represented a loss to farmers. No cereal other than barley was found in the gizzards, which probably means that only barley fields were worth exploiting at this time, either because they were the only grain fields available or because other types were too far away to exploit efficiently.

Although most authors (see above) have recorded vegetable food to be far more common than animal food in rook diet the proportion of vegetable food noted in this study (> 90%) is the highest of all. One reason for this could be that, as mentioned, the number of invertebrate items is under-represented due to the quick digestion of such food. Another possible reason is that many invertebrates were not readily available to the rooks at this time due either to the ground being too hard in which to probe or to other adverse soil conditions. Certainly, most of the invertebrate items recorded are surface as opposed to sub-soil living ones.

As rooks hatch asynchronously the correlations between nestling weights and amounts of food brought to them are to be

expected. There was much variation in the size of the nestlings in this study (see Table 6.4, p. 257) so the larger ones were probably those which hatched earliest from clutches, while the smaller ones hatched later. Early hatched nestlings, therefore, get fed by their parents while other eggs have still to hatch and so these will be larger than their siblings when the latter eventually hatch. This size difference will persist during the nestling stage as the larger nestlings succeed better than small ones at being fed by the adults. This is true not only of rooks but also of other asynchronously hatching species and is a mechanism to ensure the survival of at least some of the nestlings during possible times of food shortage (Lack 1947b, 1954). The gizzards of some of the smaller nestlings under study contained little food and so these birds may have starved to death had they not been shot.

The negative relationship between nestling wing length and amount of stones and grit in the gizzard is rather more puzzling. A likely explanation, however, is that as nestlings mature they eventually become able to disgorge pellets containing indigestible gizzard contents. Young peregrine falcons Falco peregrinus cast these only after they are approximately 22 days old (Ratcliffe 1980). The smaller nestlings in this study, therefore, probably retained all of the mineral material which accompanied their food, while the older, larger nestlings had ejected this in pellets. Alternatively, many of the stones in the larger nestling gizzards may have been ground finely enough to be eliminated via droppings.

Which fields were available to the rooks of rookery 50/07 at this time is not known, but a look at Table 5.1 (pp. 230-235) shows that in May 1978 along the transect area between St. Andrews and Guardbridge the only fields available to an appreciable extent were grass and braird ones. Moreover, rooks used these two field

types, along with plough in progress and sown barley fields, more than any others. It is unlikely that the fields available to the adult birds of rookery 50/07 were much different. Sown barley and braird fields were certainly used by them, as evidenced by the amount and nature of the grain found in the gizzards of their offspring. Grass fields are the most likely places where the invertebrate items (e.g. crane flies, leatherjackets, beetles and snails) were taken, giving further support for the view of the rook as primarily a grassland forager (see Lockie 1955, 1959, chapter 4), and this despite the fact that the remains of earthworms were not discovered in the gizzards of this study.

Table 6.1. Food of young rooks. An 'x' indicates the presence in the gizzard of that food. Other entries represent minimum numbers of individual items. Abbreviations: ad. - adult; Pl - plant; Malloph. - Mallophaga (bird lice); Thysan. - Thysanoptera (thrips); Coleop. - Coleoptera (beetles); Carab. - Carabidae (ground beetles); Scarab. - Scarabaeidae (dung beetles); Staphyl. - Staphylinidae (rove beetles); Lepidop. - Lepidoptera (entries refer to caterpillars); Tipulid. - Tipulidae (crane flies); LJ - leatherjackets (larvae of crane fly). Maggots are larvae of Diptera (flies). Unspecified entries for Coleoptera and Diptera refer to unidentified adults of these orders. 'Inverts ?' are unidentified invertebrate remains.

	Rook																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Barley	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Pl roots	x			x	x			x						x						
Seeds					1								1					6	1	
Snails								2		1			1	1			1			
Spiders					1												1			
Malloph.																				1
Thysan.											1									
Coleop.	1			x	x		1		1					1						
Carab. ad.	1	1	1		2	4	1			2		1	1				1	1	2	
Scarab. ad.				1							1									1
Staphyl. ad.					1	1		2												
Larvae							1			1	1		1	1			1			
Lepidop.		4								1										
Diptera					1													1		
Tipulid ad.		3																		1
Tipulid LJ				4	13															
Maggots		1		1																
Carrion																	x			
Inverts ?	x	x			1		2			x							1	x		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20

Table 6.2. Dry weights (g) of various material found in young rook gizzards.

Rook	Veg.	Anim.	Min.	Shells	% of food contents Veg.	Anim.
1	3.139	0.003	2.725	-	99.90	0.10
2	1.750	0.106	4.382	-	94.29	5.71
3	1.391	>0.000	0.078	-	<100.00	>0.00
4	3.319	0.206	-	-	94.16	5.84
5	1.790	0.130	2.030	-	93.23	6.77
6	5.557	0.016	0.286	-	99.71	0.29
7	4.250	0.008	2.717	-	99.81	0.19
8	0.041	0.051	1.641	0.728	44.57	55.43
9	0.471	0.001	0.504	-	99.79	0.21
10	4.215	0.029	0.129	0.074	99.32	0.68
11	3.104	0.005	1.783	-	99.84	0.16
12	0.894	>0.000	4.725	-	<100.00	>0.00
13	1.257	0.008	2.257	0.387	99.37	0.63
14	4.019	0.003	1.272	0.021	99.93	0.07
15	0.053	-	0.016	-	100.00	0.00
16	0.562	-	0.147	-	100.00	0.00
17	1.335	0.005	1.250	1.333	99.63	0.37
18	2.612	0.004	2.847	-	99.85	0.15
19	1.572	>0.000	1.513	-	<100.00	>0.00
20	0.129	0.001	0.034	-	99.23	0.77
Means	2.073	0.003	1.517	0.127	96.13	3.87

Table 6.3. Volumes (cm^3) of various material found in young rook gizzards.

Rook	Veg.	Anim.	Min.	Shells	% of food contents Veg.	Anim.
1	4.00	<0.25	1.50	-	>94.12	<5.88
2	1.00	0.50	2.25	-	66.67	33.33
3	1.25	>0.00	0.25	-	<100.00	>0.00
4	3.00	0.50	-	-	85.71	14.29
5	2.00	1.00	1.50	-	66.67	33.33
6	4.50	0.25	0.50	-	94.74	5.26
7	4.50	0.25	1.50	-	94.74	5.26
8	0.50	0.25	1.00	0.50	66.67	33.33
9	0.50	>0.00	0.50	-	<100.00	>0.00
10	3.25	0.50	0.25	0.25	86.67	13.33
11	3.00	0.25	1.00	-	92.31	7.69
12	0.75	>0.00	2.50	-	<100.00	>0.00
13	1.00	<0.25	1.00	0.50	>80.00	<20.00
14	3.00	<0.25	1.00	>0.00	>92.31	<7.69
15	0.25	-	0.25	-	100.00	0.00
16	1.00	-	0.25	-	100.00	0.00
17	1.50	>0.00	1.00	1.00	<100.00	>0.00
18	2.75	>0.00	1.50	-	<100.00	>0.00
19	1.25	>0.00	1.00	-	<100.00	>0.00
20	0.25	>0.00	0.25	-	<100.00	>0.00
Means	1.96	0.21	0.95	0.11	91.03	8.97

Table 6.4. Measurements of young rooks. Weight is in grams. Other measurements are in millimeters.

Rook	Weight	Wing length	Bill length	Bill depth
1	362	127	43.2	12.1
2	377	225	-	-
3	408	237	52.3	14.8
4	439	235	52.0	14.9
5	465	231	54.4	13.5
6	544	252	56.1	16.4
7	477	194	52.6	15.8
8	270	157	43.9	12.7
9	430	228	52.4	15.6
10	479	233	57.3	14.0
11	475	202	50.6	16.6
12	475	208	54.9	15.4
13	429	226	53.6	14.8
14	456	205	52.6	13.8
15	301	218	50.2	13.3
16	444	250	55.5	15.5
17	432	205	47.4	14.0
18	-	154	46.3	13.7
19	380	193	47.7	11.4
20	384	244	50.8	14.3

Chapter 7. Competition and dominance in captive rooks and carrion crows

INTRODUCTION

The ability of an individual organism to compete favourably for food with other individuals (of its own or other species) is one of the most potent factors affecting the fitness of that individual. In order to avoid competing with others, or to attain competitive dominance over them, subordinate species, or individuals, have several options. Evolution may favour larger body size, perhaps with larger bodily appendages, for use in fighting; or the individuals could disperse and attempt to settle in a new area or habitat with fewer competing species; or they could change their diet, which again could involve concomitant changes in external morphology and also internal physiology. These solutions are, however, costly in evolutionary terms, particularly for the individual animals concerned. A more parsimonious path for evolution to take, and one which confers advantage on the individuals involved, is for the latter to change some aspect of their behaviour in order to exploit a resource which is at risk of being exploited by individuals of their own or other species. One possibility is to become sociable, or at least to become part of a group, and so gain advantage from 'safety in numbers'. This could, but need not necessarily, involve cooperation between subordinate animals.

It is generally assumed that dominant animals always have priority over subordinate animals when access to resources is at stake. For example, in flocks of domestic hens, in which there is usually a very well-structured dominance hierarchy, it is the dominant birds which have priority of access to food, nest sites,

mates, etc. (Wilson 1975). In more complicated social organisations, however, subordinate individuals may get more food than one would expect of low ranking animals. In cooperatively breeding Arabian babblers Turdoides squamiceps, for example, dominant male birds signal their dominant status by passing food to subordinate males (Zahavi 1977). This chapter presents the results of an investigation into the relationship between dominance and feeding performance in a group of captive rooks and carrion crows. In it I present evidence showing that a subordinate corvid need not have a lower food intake than a dominant one in a one to one competitive situation, and that the food intake of a subordinate individual might actually improve when in competition with a dominant if there is another subordinate bird present.

METHODS

The subjects of the observations were an unmated pair of adult carrion crows (♂ Cc and ♀ Cc) and two adult rooks aged >10 yr and >5 yr (♀ R and Pi respectively), all of which had spent the greater part of their lives in captivity. The two species were normally housed separately.

The observations were made on 6 days between 24 August 1978 and 20 September 1978, and consisted of 1 h morning sessions. For 24 h prior to a session the birds to be observed were given no food, though they had free access to water at all times. In a session 50 g of mealworms Tenebrio molitor per bird to be observed, were provided in a shallow dish in the centre of one discrete section of the aviary where the observations were made (see chapter 9 for a description of the aviary, one third of which was used for the observations reported in this chapter). Each session involved watching two or three birds

and recording the time each bird spent feeding at the bowl or just standing at the bowl (in a position to defend it). The method used for this was instantaneous sampling (Altmann 1974) at intervals of 10 sec. Also recorded was the absolute number of pecks by each bird which resulted in capture of at least one mealworm, and the nature and absolute number of agonistic interactions that took place between them.

Agonistic encounters could be of 6 types: 1) threat - one bird threatens another using one or more of the species conventional threat postures (see Lockie 1956a, Coombs 1978); 2) stab - the bird attacking makes a thrusting movement with the bill towards the victim; 3) retreat - one bird withdraws as another approaches, the latter showing no overt (to the human eye) signs of aggression; 4) chase - after a threat or stab, usually, when the attacker runs after the victim who is running away; 5) flight - as chase, but instead of running the birds fly; and 6) fight - prolonged (>3 sec), agonistic physical contact between birds, one of whom may, or may not, retaliate. The criterion for one bird to be dominant to another was that it displaced the other more often than it was itself displaced by the other (i.e. won more agonistic encounters than it lost against the other).

Each bird was paired with every other for the purposes of recording, making 6 sessions when only two birds were observed. Observations were also made between both rooks and each carrion crow, making a further 2 sessions when three birds were observed. Thus the line-up for the 8 sessions looked like this:

Intraspecific	Interspecific (1:1)
♂ Cc vs. ♀ Cc	
♀ R vs. Pi	♂ Cc vs. ♀ R
Interspecific (2:1)	♂ Cc vs. Pi

♀ R vs. Pi vs. ♂ Cc ♀ Cc vs. ♀ R

♀ R vs. Pi vs. ♀ Cc ♀ Cc vs. Pi

More observations than this should have been made, observations which would have included replications and controls involving more birds. The investigation was terminated prematurely, however, because the birds were becoming stressed by the conditions under which it was being carried out. Observations were made from a hide erected outside the aviary, and scoring was done on a checksheet.

RESULTS

In all four sessions involving ♀ Cc this bird cached mealworms frequently. This mostly took the form of placing a beakful of mealworms in a corner of the aviary and covering the cache with contour feathers picked up from the aviary floor (and which were the only suitable material available for the purpose in the aviary). The other carrion crow, ♂ Cc, did not cache, and ♀ R and Pi only cached in the session when both of them were present with ♂ Cc. Caching by the rooks tended to be in cracks in the aviary structure rather than corners, and again, contour feathers were used to cover the mealworms. Agonistic encounters which took place at caches were included in the analysis. If a bird stole part, or all, of another bird's cache then these pecks were included in the analysis, but pecks made by a bird at its own cache were not, as these would already have been scored while the bird was at the feeding bowl.

All pecks taken by all birds at the food bowl resulted in the successful capture of a minimum of one mealworm. Therefore pecks = successful pecks in the ensuing discussion.

In the two intraspecific sessions ♀ R was dominant to Pi (5

agonistic wins against 0) though Pi did take more pecks at the mealworms (63 against 43); and ♂Cc was dominant to ♀ Cc (16 agonistic wins against 0), though again the subordinate bird had more pecks (386 against 127). In the two intraspecific and four interspecific 1:1 sessions 26 (52%) of all agonistic acts were threats followed by withdrawal of the threatened bird.

In the 1:1 situations, i.e. one rook against one carrion crow, each carrion crow was dominant to each rook, and this remained so in the 2:1 situation (two rooks vs. one carrion crow), though the frequency of agonistic encounters increased (Fig. 7.1, p. 267). In the 2:1 situations, carrion crows won all 57 agonistic interactions, 43 (75%) of which were threats followed by withdrawal of the rook involved. Figures 7.2 and 7.3 (p. 268) provide details of agonistic wins and losses of all four birds.

Despite this clear dominance by carrion crows over rooks, both rooks, in the session with ♂Cc, actually increased the number of pecks they took when in the corresponding 1:1 situations with this carrion crow, ♂Cc 's number of pecks decreasing (X^2 = 19.92, 1 d.f., $p < 0.001$ and X^2 = 18.04, 1 d.f., $p < 0.002$ for ♀ R and Pi respectively).

♀ R also took significantly more pecks in the 2:1 situation with ♀ Cc than in the corresponding 1:1 situation with ♀ Cc, the latter's number of pecks being less (X^2 = 29.37, 1 d.f., $p < 0.001$).

Pi actually took less pecks in the 2:1 situation with ♀ Cc than in the 1:1 situation (as did ♀ Cc), but this was not significant (X^2 = 2.11, 1 d.f., $p = 0.15$).

In the 2:1 situation with ♂Cc, both rooks actually managed more pecks than ♂Cc, but they still took less than ♀ Cc when against this bird in the 2:1 situation (Fig. 7.4, p. 269).

Figure 7.5 (p. 270) shows the average % change in the

number of pecks taken by each bird as a result of being in a 2:1 situation as opposed to a 1:1 situation.

Each rook spent a greater (but not significantly so) proportion of its time feeding (in terms of the number of positive scans) in the 2:1 situation than in the corresponding 1:1 situation when against ♂Cc ($X^2 = 1.34$, 1 d.f., $p > 0.05$ for ♀ R and $X^2 = 3.41$, 1 d.f., $p = 0.06$ for Pi), but similar comparisons when against ♀ Cc revealed little change (Fig. 7.6, p. 271).

The average peck rate (here defined as the number of pecks taken per number of scans for which the bird was at the bowl feeding) for the carrion crows decreased from 4.35 in the 1:1 situations to 3.43 in the 2:1 situations but for the rooks only from 5.00 in the 1:1 situations to 4.47 in the 2:1 situations. Thus, having another low ranking individual present makes little difference to the peck rate of a subordinate corvid, whereas another subordinate present can mean a decrease in the peck rate of the dominant individual present. In addition, the proportion of time spent at the bowl not feeding (i.e. in a position to defend it or actually defending it) was greater for ♂Cc and less for ♀ R in the 2:1 situation as opposed to the corresponding 1:1 situation but this was not significant. Similar comparisons involving Pi and both carrion crows, and ♀ R and ♀ Cc (where few changes were also evident) were not significant.

DISCUSSION

These observations, made in the restricted conditions of captivity, show primarily that there need be no clear relationship between dominance, as ascertained by scoring agonistic acts, and the extent of resource exploitation in competitive situations. The observations also show that it can be advantageous to a subordinate

bird to have a another subordinate present when in a competitive situation with an individual of more dominant status. The rooks in this study were able to improve their feeding performance when competing with a carrion crow. They were able to do so by spending slightly more time feeding (against one of the carrion crows), by maintaining their peck rate at a level close to that when there was no other rook present and, to some extent, by spending less time not feeding when at the food bowl while the carrion crow spent more of its time at the bowl defending it. While rooks are subordinate to carrion crows it may not be concluded from these observations that the rook as a species is able in a wider sense to attain competitive dominance over carrion crows by virtue of being in a group. This possibility remains to be investigated thoroughly. The crucial control observations which might have thrown some light on this matter were not carried out in this study. These are the conditions in which both carrion crows plus each rook individually are observed, and also all four birds together (i.e. ♂Cc vs. ♀ Cc vs. ♀ R, ♂Cc vs. ♀ Cc vs. Pi and ♂Cc vs. ♀ Cc vs. ♀ R vs. Pi). The study would also have benefitted from replications of the observations which were carried out. While these observations (controls and replications) should have been part of the study the subjects, as mentioned, were becoming stressed by the conditions under which the observations were being carried out (prolonged period of no food followed by competitive interactions with other birds).

The mechanism whereby the subordinate birds fared better when there was another present seemed to be that the dominant bird involved had an 'attention problem'. That is, the dominant experienced difficulty in displacing two subordinates at a time, and while it was displacing one from the food bowl the other would dart in and feed until it was displaced, so leaving the bowl free for the

other subordinate, and so on. There were occasions however when both subordinates were displaced simultaneously. There was no indication that the subordinate birds were acting in any organised, purposeful or cooperative manner - they were merely being opportunistic.

The conditions under which this study was conducted (i.e a localised, abundant food supply to be shared by more than one species) also prevail, for part of the year at least, in the wild. Abundant, localised patches of food attractive to both rooks and carrion crows exist in the wild as cereal stacks, dung heaps, garbage and even certain field types (see chapter 4). There are overlaps (which in some cases are not insignificant) in the diet of the two species (Lockie 1956b, Holyoak 1968), and also in their use of the habitat for foraging (see chapter 5).

A pair of carrion crows can expel up to 24 other conspecifics from their territory (Coombs 1978), and therefore can presumably expel as many smaller birds such as rooks or jackdaws. The cost/benefit ratios associated with such attacks probably depend on the value of the resources at stake. The present observations indicate that these ratios may also be affected by the number of competing individuals present. It is not advantageous for a dominant bird to displace one rook from a food source if, while it is doing so, it allows another subordinate to gain access to the food. Low levels of aggression in the wild between rooks and carrion crows (personal observation) may indicate that the cost/benefit ratio for carrion crows to attempt to expel rooks from feeding grounds is rarely less than unity. Therefore, where niche overlap between the two species exists they may coexist in relative peace due to the reluctance of carrion crows to displace large numbers of rooks from their territories. Similarly, flocks of young (or non-breeding) carrion crows are able to withstand interference from older, dominant

breeders if they are part of a large group (Charles 1972).

So the results presented here are consistent with the possibility that an advantage of grouping behaviour in corvids is that they are able to coexist with dominant individuals and to compete more favourably with them. In fact Roell (1978) observed rooks (and also magpies) to "join forces and subsequently drive off a crow". Given that larger animals tend to be dominant to smaller ones (Wilson 1975) flocking would generally seem to be an effective strategy for increasing the competitive ability of a subordinate species to the detriment of a dominant one. Although this cannot be concluded from the present study, the observations suggest that sociality could indeed be a mechanism whereby competitive dominance over solitary, dominant species is realised.

Though observations are few, it has previously been shown that dominance by groups of animals can be achieved over either individuals or smaller groups, of the same, or other species. Much of the evidence is anecdotal or merely suggestive, but various vertebrate groups are represented. These include fish in both inter- and intraspecific encounters (Robertson et al 1976); ungulates intraspecifically (Miller and Denniston 1979); carnivores interspecifically (Estes and Goddard 1967, Kruuk 1972, Lamprecht 1978, Schaller 1972, Eaton 1979a,b) and intraspecifically (Eaton 1979b); and primates, both for interspecific (Jolly 1966), and intraspecific interactions (Lindburg 1971, Wrangham 1980). Among birds, individuals of the following have been observed competing favourably with others when part of a larger group than those they are in competition with - Gambel's quail Lophortyx gambelii (interspecifically, Fisler 1977); cedar waxwing Bombycilla cedrorum, American robin Turdus migratorius and starling (all interspecifically, Moore 1977); Gymnorhina, Dacelo, Aphelocoma,

Phoeniculus, Porphyrio and Pomatostomus spp. (all intraspecifically, Brown 1978); tricolored blackbird Agelaius tricolor (interspecifically, Orians and Collier 1963); Carolina chickadee Parus carolinensis and golden-crowned kinglet Regulus satrapa (both intraspecifically, Morse 1970). Among corvids, Rowley (1973) has noted inter- and intraspecific examples in Australia, and Bossema et al (1976) and Roell (1978) have suggested that rooks and jackdaws may be sociable in order to be able to coexist with carrion crows. More recently, Vines (1981) has shown that larger flocks of magpies can spend significantly more time feeding in carrion crow territories than smaller flocks can. Of course there may be other (not necessarily less important) functions of being part of a group (Bertram 1978). Further investigation of the possibility that sociality in subordinate species may be a mechanism by which competitive advantages over dominant species might be gained could prove fruitful.

Although the results of this study reveal a linear dominance hierarchy among the four birds this did not enable one to predict which birds would be more successful in terms of acquiring food from the bowl. Why this should be the case is puzzling as aggressive dominance is usually seen as the mechanism whereby access to resources is ensured (Wilson 1975). As mentioned, the subordinate birds in the study were able to improve on their feeding performance by being opportunistic, and in the sessions involving a single species (♂Cc vs. ♀ Cc and ♀ R vs. Pi) the subordinate bird again was being somewhat opportunistic. It would appear that the subordinate birds in these sessions (♀ Cc and Pi) were capturing mealworms whenever they could as they were not able to predict if or when they would get another opportunity to feed on them. The other birds (♂ Cc and ♀ R), by virtue of being dominant, could afford to feed at will.

The subordinate birds may therefore have been attempting to take food surplus to their requirements. This is in some measure supported by the fact that the alpha individual in this group of corvids (O Cc) never cached mealworms, while all of the other birds did, thereby attempting to ensure a supply of food when the main source was unavailable (either by depletion or by being defended by dominant individuals). Dominance in this investigation was perfectly correlated with the weight of the birds so the less heavy birds may also have been more highly motivated to feed ("hungrier"), as weight loss over the food deprivation period would have been relatively more severe for these lighter, subordinate individuals.

Given the small number of birds observed, and the fact that no replications of the observations were made, individual differences in the birds' life histories, rearing conditions, etc. may have contributed to the unusual relationship between dominance and feeding performance, rather than any general biological rules governing social interaction. It is also worth commenting here on the fact that of the 20 recorded agonistic acts which might be termed highly motivated (i.e. required the expenditure of higher amounts of energy), viz. flight, chase and fight, only 1 (5%) occurred between non aviary companions (i.e. between rooks and carrion crows). This shows that relationships between aviary companions were likely to have been stabilised before these observations took place, while those between non aviary companions required a degree of interaction between the birds in order for each to assess the others' status/competitive ability. In the 2:1 sessions here the dominant bird had to assess the abilities of both other birds, while each subordinate, having been housed together with the other, would only have had to assess the ability of the dominant bird. It is possible that the subordinate birds were able to improve their feeding

performances by virtue of having the ability of fewer strange competitors to assess. Their improved performance was at the expense of the dominant bird who was kept busy assessing the abilities of two unknown competitors.

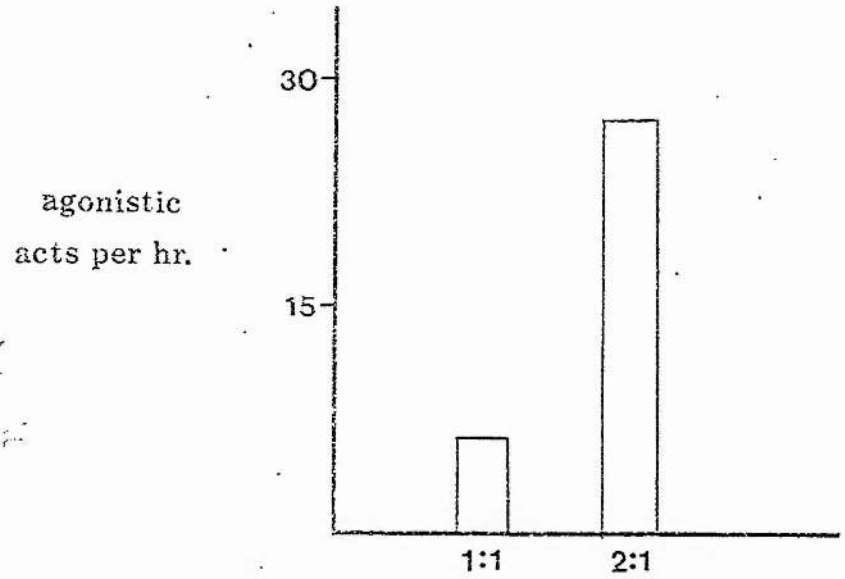


Fig. 7.1 The frequency of agonistic interactions between carrion crows and rooks in the four interspecific 1:1 (one rook vs. one crow) sessions and the two interspecific 2:1 (two rooks vs. one crow) sessions.

Losses

Wins	♂Cc	♀Cc	♀R	Pi
♂Cc		12 t 3 r 1 c 16	1 t 1 fl 2	7 t 1 r 8
♀Cc	0		4 t 4 fl 1 r 1 c 10	2 t 2 fl 2 c 6
♀R	1 r 1	0		3 r 2 s 5
Pi	0	2 r 2	0	

Fig. 7.2 Details of agonistic wins and losses in the two intraspecific (♂ Cc vs. ♀ Cc and ♀ R vs. Pi) sessions and the four interspecific 1:1 (each rook vs. each crow) sessions. The figure in the bottom right corner of each square is the sum of the different types of interaction. These were threat (t), retreat (r), stab (s), flight (fl) and chase (c).

Losses

Wins	♂Cc	♀Cc	♀R	Pi
♂Cc			11 t 1 r 12	15 t 1 r 16
♀Cc			12 t 7 fl 2 r 1 c 1 ft 23	5 t 1 r 6
♀R	0	0		1=
Pi	0	0	1=	

Fig. 7.3 Details of agonistic wins and losses in the two interspecific 2:1 (two rooks vs. one crow) sessio The figure in the bottom right corner of each squ is the sum of the different types of interaction. These were threat (t), retreat (r), flight (fl), chase (c) and fight (ft). The entry, 1=, for ♀ R and Pi signifies a brief agonistic clash of bills between these birds, neither of whom could be sai to have won or lost the encounter.

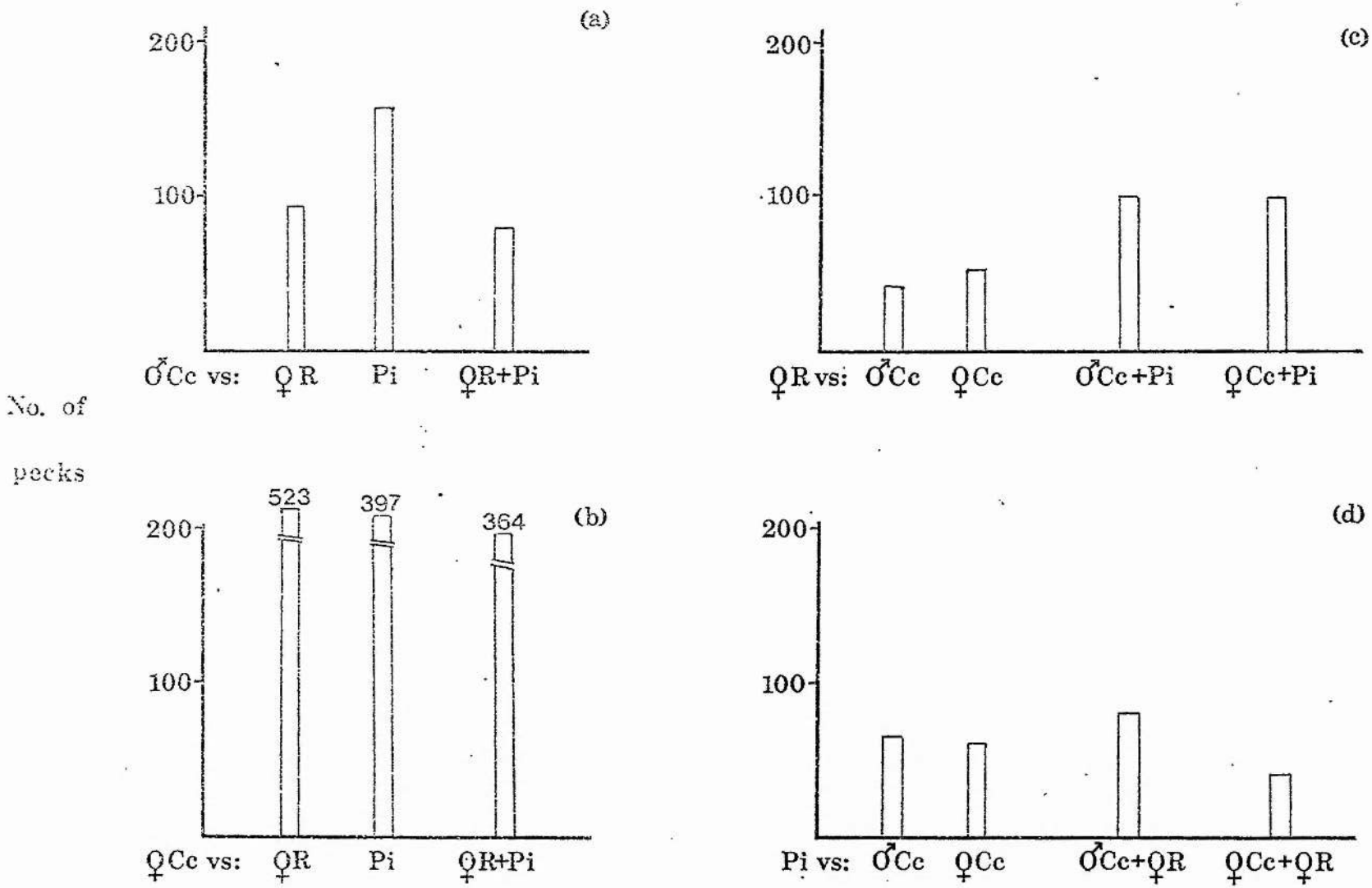


Fig. 7.4 The number of successful pecks taken by ♂ Cc (a), ♀ Cc (b), ♀ R (c) and Pi (d) in all interspecific (1:1 and 2:1) sessions in which these birds were involved.

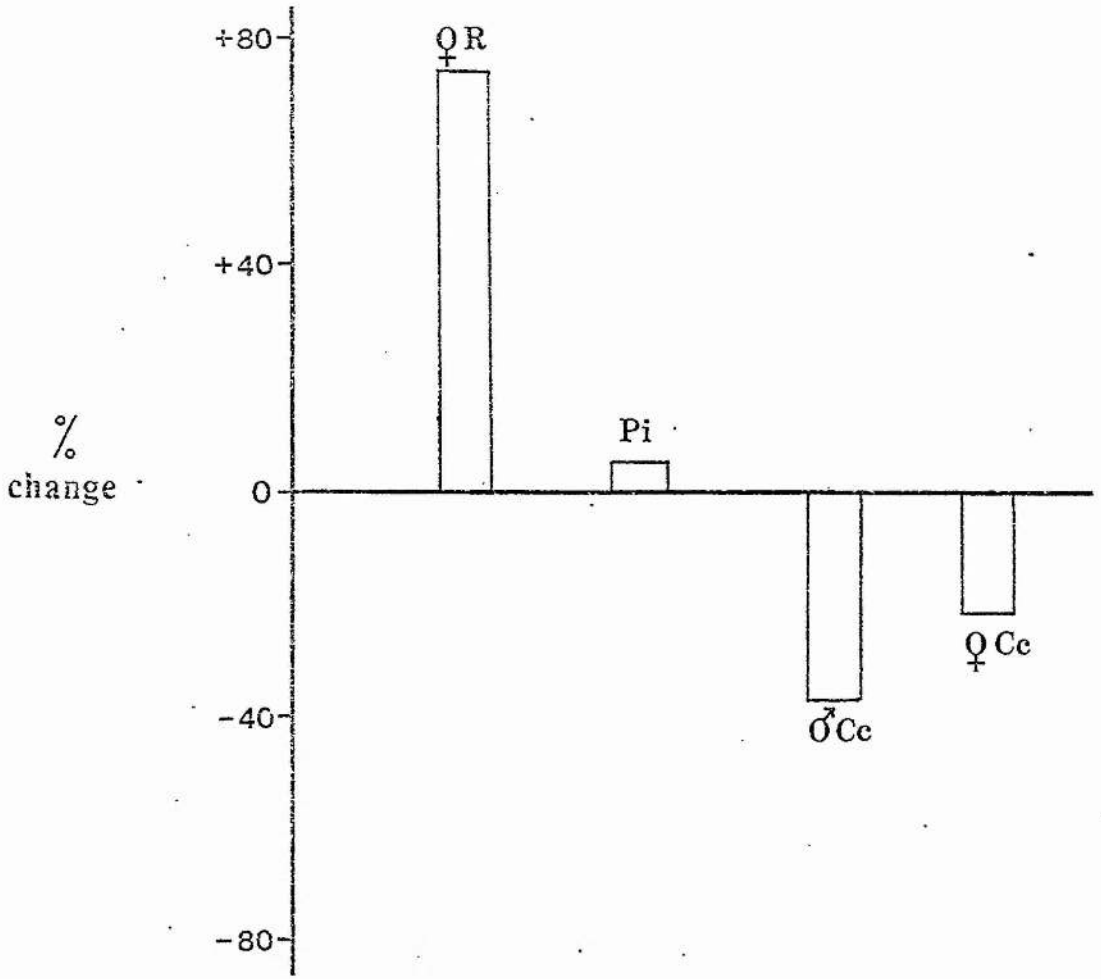


Fig. 7.5 The average percent increase or decrease in the number of successful pecks each bird made from the interspecific 1:1 (one rook vs. one crow) sessions to the interspecific 2:1 (two rooks vs. one crow) sessions.

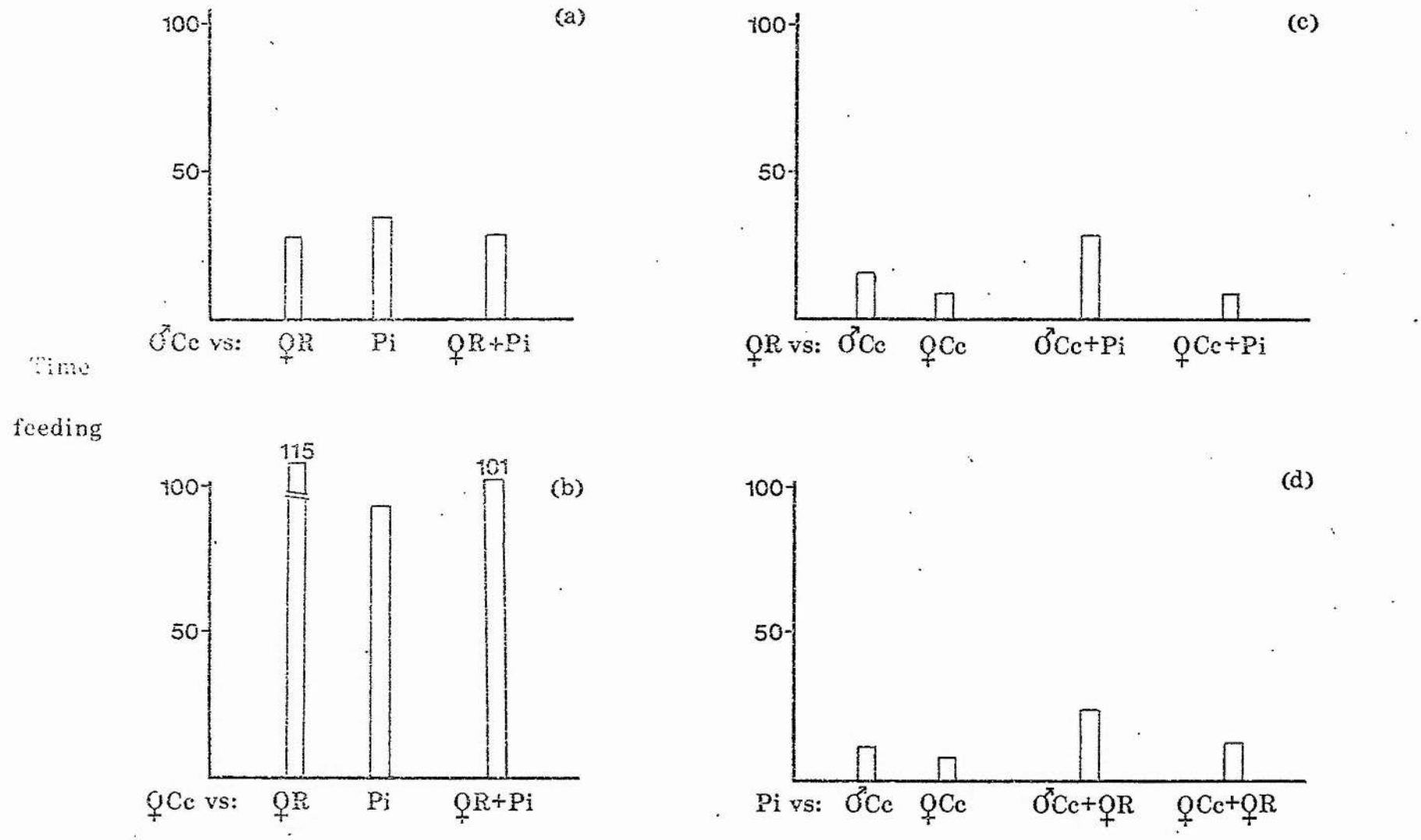


Fig. 7.6 The time spent feeding (i.e. the number of 10 s scans positive for feeding) by ♂ Cc (a), ♀ Cc (b), ♀ R (c) and Pi (d) in all interspecific (1:1 and 2:1) sessions in which these birds were involved.

Chapter 8. A review of avian tool-use

INTRODUCTION

Arguably, food caching by corvids when the cache is covered with material (see previous chapter) is an instance of tool-use. Recently, consideration has been given to the general ecological conditions under which animal tool-use arises (Beck 1980). General reviews of the subject have also appeared in Alcock (1972), Beck (1975) and van Lawick-Goodall (1970). Boswall (1977, 1978, 1979, 1981, 1983) gave a comprehensive account of tool-use in birds. This chapter serves as an introduction to a clear-cut example of rook tool-use to be reported in chapter 9. In it I present a review similar to Beck's (1980), but in a little more detail with particular reference to birds. More birds are known to use, or to have used, tools than any other animal group. It is not a theoretically comprehensive review as it deals mainly with ecological aspects of tool-use. While interesting and important questions arise when considering tool-using behaviour, such as those about animal cognition and awareness and the cultural transmission of behaviour, these lie largely outwith the scope of the present discussion. Similarly, no particular emphasis is given here to ontogenetic versus phylogenetic factors important in the development of tool-use, but the following chapter does address the possible origins of rook tool-use.

Defining tool-use has always been a problem. The definition I have adopted here is that of Beck (1980), though of the examples of tool-use to be discussed, none would be excluded as such by an earlier definition given by Alcock (1972). Beck defines tool-use as "the external employment of an unattached environmental

object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool." With respect to this definition there are, to date, 52 species of bird on record as having used a tool. There is a problem in that some of the examples to be considered have only been described as "apparent" tool-use, and a few species have not actually been observed to successfully use a tool. These, however, are few in number, and I have included them as examples of tool-use for the sake of being exhaustive. It is likely, though, that the example of the black-breasted buzzard, Gypoictinia melanosternum, has its roots in the folklore of Australian aboriginals (J. Boswall, personal communication) and may not be a serious candidate as an example of tool-use. One must also bear in mind that alternative explanations may exist for what I, and others, have accepted as tool-use.

Few species use tools regularly as part of their usual behavioural inventory (see next chapter for some that do), and the fact that one or two individuals of a species have been observed tool-using is not necessarily an indication that all individuals of the species possess the ability to tool-use. It does suggest that some other individuals do, however, and that there is always the possibility that a tool-using behaviour may be incorporated into a species ethogram by behavioural or other mechanisms. This is why, in the ensuing discussion, I sometimes refer to a "tool-using species", meaning a species of which at least one individual has been observed using a tool.

Table 8.1 (pp. 283-286) lists the 52 tool-using species and their respective performances, and is based largely on Boswall (1977, 1978, 1979). Table 8.2 (pp. 287-288) classifies each tool-using

species according to various criteria regarding its life history/ecology.

The species

Notable in Table 8.1 (pp. 283-286) is the fact that parrots (Psittidae) and crows (Corvidae) are well represented, the genus Corvus being especially rich in tool-using species. Individuals of both of these groups generally possess a high degree of learning ability and are explorative and playful birds, qualities which enhance both the likelihood of discovery of tool-use and also of its maintenance if it is sufficiently rewarding. Worthy of note also are the other genera which have more than one tool-using species viz. Turdus, Parus, Sitta, Geospiza and Cactospiza. These last two are Galapagos finches, and it is possible that they share a common ancestor which was a tool-user, the behaviour being retained after speciation. More likely, however, is that interspecific observational learning has occurred, especially in the light of the fact that very few individuals of Galapagos finches other than C. pallida have been known to tool-use. It is less clear why Sitta, Parus and Turdus should each have two tool-using species. Observational learning can be ruled out in all three cases as the two Sitta species perform different tool-using activities and neither the two Turdus nor the two Parus species overlap geographically. Explanations based on common ancestry are unlikely in these instances also, and the reason could well be coincidence. Six species have been recorded as employing two methods of tool-use. These are the bald eagle, lesser sulphur-crested cockatoo, African grey parrot, northern blue jay, common crow and raven. These, then merit the label "intelligent" tool-users as defined by Parker and Gibson (1977) (see below). Again the crows and parrots predominate here. The

broad range of bird species in Table 8.1 (pp. 283-286) may indicate that birds are a particularly opportunistic type of animal generally.

Categories of tool-use

Table 8.1 (pp. 283-286) reveals that the 58 examples of tool-use (involving 52 species) fall into eight categories. Thirty-five were performed for feeding purposes, nine for body care, two for drinking, four for defence, three for nest-building, one for bathing, one for attracting attention and three were playful.

If one considers only those instances which occurred in captivity then the broad spectrum of categories is fairly evenly represented except for body care. The reason for this is that five parrot species have been recorded as using objects to groom themselves. Parrots, of course, frequently groom each other for social reasons as well as to remove parasites, and the opportunity for allogrooming is probably the most severe deprivation for a lone-housed parrot. A parrot caged without companions, therefore, is thwarted from having the region around its head groomed, and for this reason there is perhaps more pressure on it to find alternative means for accomplishing this task. Put another way, the rewards for discovering a novel method of having the head region groomed are greater for a parrot with no companion than one with a companion, and the novel behaviour is therefore more likely to be retained in the behavioural repertoire of the former.

Considering those instances of tool-use performed by wild individuals, only half the categories are represented, with 26 of the 33 examples involving feeding or foraging. For a wild animal, clearly, feeding is one of its most important activities, and so the situation is analagous to that of captive parrots where grooming becomes a priority activity in the face of the relaxation of feeding

or other constraints. Captivity, however, does not entail the complete absence of constraints (see below).

Geographical residence of tool-users

Table 8.1 (pp. 283-286) indicates where tool-users in the wild have been observed to do so. Ten live in Australia and the islands to the north of it, ten in the U.S.A., four in the Galapagos Islands, three in Europe, three in Africa and one in Oceania. A further species has tool-using records of individuals living in both Africa and the U.S.A. This distribution broadly reflects the intensity of ornithological research in various parts of the world, though perhaps one would have expected more examples from Europe.

Captive/wild tool-users

Table 8.2 (pp. 287-288) shows that two species, Cactospiza pallida and Corvus brachyrhynchos, have used tools in the wild and in captivity. In all, 32 species have used a tool in the wild and 22 have done so in captivity. This means that about a third of all tool-using bird species have done so only in captivity, which is a fairly high proportion even considering that captive birds are more readily observable. Living in a cage presents many problems to a non-domesticated animal, not least of which is the general impoverishment of its environment. After all, animals are adapted to living in the wild with a diversity of habitat, food abundance, climatic conditions, competitors, companions, etc. In captivity, then, the opportunities for problem-solving (which in a sense is what tool-use is) are greatly increased because the animal is more likely to find its means to some goal thwarted. Thus can the large proportion of captive tool-users be explained.

Passerine/non-passerine species and nature of the young

All but three tool-using species have nidicolous young. The respective numbers of all bird species having nidicolous and nidifugous young are difficult to obtain but the vast majority have nidicolous young. The observed numbers of each in the list of tool-users, then, probably does not differ from chance. Similarly, the ratio of passerine to non-passerine tool-using species (25:27) is probably not significantly different from the corresponding ratio for all extant species, even though passerines comprise rather more than half of these.

Feeding habitat

Of the 26 species which use, or have used, a tool for feeding purposes in the wild, 14 capture their food mainly in a terrestrial habitat, nine in an arboreal one and three in water.

Beck (1980) has discussed the idea that tool-using generally is more likely to evolve in terrestrial rather than in arboreal habitats on account of their being a wider range of potential tools available on the ground than in trees. He concluded that "There is no simple correlation between terrestriality and tool behaviour." On the face of it the distribution presented here contradicts Beck, but no firm conclusion can be reached again because expected frequencies of birds using different habitats are difficult to ascertain.

Of the eight species known to have used tools in captivity for feeding, the majority (six) are terrestrial feeders, but conjecture on the reasons for this would not be meaningful.

Diet of tool-users

Parker and Gibson (1977) identify two types of feeding

tool-user - context-specific and intelligent. In view of the connotations the term "intelligent" has re cognitive ability I will use the term context-free here instead. Context-specific tool-users have one mode of using tools confined to one type of situation, but context-free tool-users may have different modes of tool-use in different situations. Both types of tool-use are seen as adaptations for "extractive foraging" on "embedded food". Context-free tool-users, they state, will tend to be omnivorous, whereas context-specific tool-users will have a "narrow non-omnivorous diet" (see discussion by Beck, 1980).

If we consider those bird species known to have used tools in the wild for feeding purposes, Table 8.2 (pp. 287-288) shows that 13 of the 26 are mainly insectivorous, seven are omnivorous, two are carnivorous, two are piscivorous, one is granivorous and one is mainly frugivorous. This distribution agrees well with Parker and Gibson´s hypothesis. The only context-free feeding tool-user is the common crow (though this includes an example from captivity), and this is indeed omnivorous. Most of the other (context-specific) wild feeding tool-users are not strictly omnivorous. Notice, also, that the northern blue jay qualifies as a context-free tool-user, though the examples of tool-use here were performed in captivity. It is unclear whether species such as the bald eagle and the raven, who both perform two different modes of tool-use, only one each of which relates to feeding, should be categorised as context-free extractive foragers or not. Strictly speaking, they should be labelled in general terms as context-free tool-users, but with regard to their tool-using feeding activities, they should be called context-specific tool-users. This illustrates the rather limited usefulness of the phrases context-specific and context-free (or intelligent). If an animal can be reliably labelled as a context-specific or a

context-free feeding tool-user then hypotheses regarding its diet may be formulated comparatively safely, but if it qualifies as a context-free tool-user (i.e. if, say, it employs tools in different ways for different purposes, one of which at least does not relate to feeding), then hypotheses about its likely diet become meaningless.

Another difficulty here (and one that pervades speculations on tool-use generally) is that it is all too easy to invoke tautologies when discussing the foraging method of tool-users. It is almost a truism to say that habitual tool-using feeders are "extractive foragers". If they were feeding on a more accessible prey item which was encountered "in the open" then they would probably not need to use tools in order to capture it. Do tool-users use a tool because they are extractive foragers, or are they extractive foragers because they use a tool?

Mainland/island tool-users

Of the 32 wild tool-using species 17 live on the mainland and 15 live on islands. Again, the exact ratio of continental to island dwelling species is difficult to gauge, but there will be an extreme preponderance of continental ones, which makes the observed ratio of continental to island tool-users unlikely to happen by chance alone.

Individuals (of any taxon) colonising an island are likely to find themselves ill-adapted to any niche they attempt to fill on that island. This is especially true of remote islands. The pressures on these animals to adapt will be great, and this pressure will be exerted by both the nature of the available habitats (which will be fewer in number than on the mainland) and the number of potential competitors already established on the island. In fact, most individuals arriving on an island will probably not survive, and

this is evidenced by the high extinction rate and greater turnover of species on islands (MacArthur & Wilson 1967). Any adaptation that enhances the propensity of an individual animal to develop novel and ecologically appropriate behaviour patterns, which may include tool-using behaviour, will be selected for, but it is likely to be of even more crucial importance on an island, and here will lead to very swift selection. The rewards of adapting, as well as the pressures to adapt, then, are great on islands. The case is perhaps analagous to that of captive tool-users in that thwarting influences in the environment are more likely to be encountered by an animal, and are paramount in governing the development of problem-solving behaviour.

DISCUSSION

The "uncharacteristic niche theory" as Beck has called it has been criticised by the same author as being tautologous, and probably rightly so. I stated above that the extractive foraging on embedded food hypothesis is also somewhat circular. It is extremely difficult to avoid these tautologies when considering tool-use. The problem still remains one of identifying the special circumstances under which tool-use arises, and not just tool-use in a feeding context but tool-use generally. The most obvious similarity is that they are all examples of problem-solving where the solution involves the novel use of some object. So an important condition for tool-use to arise is that there is some problem facing the animal, and that this problem requires to be solved. Once this is recognised then we may begin to look at the possible situations where animals are more likely to encounter more problems than they would normally. Apart from living in captivity and living on, or colonising, islands another situation which provides more problems for an animal than

normal is when that animal is injured. Injured animals are already on record as having solved problems in novel ways, e.g. underwing head scratching by injured birds who, under normal circumstances, employ overwing scratching (Simmons 1961).

These three conditions (captivity, island living and injury) under which an organism is more likely to find itself thwarted in achieving a certain goal may be said to apply generally to any animal. For a more precise identification of specific circumstances under which animals might be faced with problems one must have a reasonable knowledge of the behaviour, ecology and overall life-history of these animals in order to identify their priority activities. I pointed out above that, other things being equal, a lone-caged highly social bird such as a parrot would be more deprived than a lone-caged normally solitary living one, or at least one which did not have allogrooming as part of its ethogram. A similar argument was made for feeding in wild birds being a priority activity.

Several questions may be asked when trying to account for the evolution of tool-use, or to predict when it will arise: Is the organism living under conditions which are generally likely to present it with problems to be solved over and above the problems which are usually encountered by individuals of the species as a whole? ; Are priority activities of the animal thwarted? If the answers to these two questions are in the affirmative it does not necessarily mean that the animal is inhabiting an uncharacteristic niche. The solutions to problems could well be part of the overall relationship between the animal and its niche. Affirmative answers, though, mean, I believe, that two very important conditions conducive to the emergence of tool-use exist. Another question one must ask is: What cognitive abilities does the animal seem to already possess

in order to solve problems in certain ways? Answering the first two questions is comparatively simple to answering this third one. The third leads into unknown areas of animal biology (Beck 1980), and it is perhaps towards this area that attention should be channelled. What is required is an analysis of the organism's ethogram to identify cognitive processes that it would seem to be executing in the course of its everyday existence. This requires knowing fully the demand characteristics of the problems that animals are known to be able to solve in the wild - for example, what cognitive operations are apparently necessary in finding a patch of food? Once questions like these are asked and eventually answered then we will be in a position to say that that animal will or will not be capable of solving specific problems in specific ways. Once a tool-using technique has been discovered by an individual its spread or otherwise in the population will be governed by the same sorts of factors that govern the original innovation, and those that govern the spread of non tool-using behaviours, with the degree of ability for observational learning by the species being particularly important. There will have been many more cases of extinction because animals were not capable of solving a problem than there have been tool-using solutions to problems.

Table 8.1. A list of tool-using bird species. A brief description of each tool-using behaviour is given for all species. Letters in bold type after each entry indicate the category into which each tool-using performance falls. These are: F - feeding; BC - body care; Def. - defence; NB - nest building; P - play; Dr. - drinking; Bath. - bathing; A - attention seeking. Those in parentheses indicate performances by wild individuals. The geographical location of wild tool-users is also indicated. 'Australia' includes the islands north of Australia (New Guinea group). The underlined number at the end of each entry indicates the source of the observation. Sources are given at the end of the table.

Double-crested Cormorant Phalacrocorax auritus	Feather used to apply preen gland secretion to wing. (U.S.A.) **(BC)** 1
Green Heron Butorides virescens	Feather and food used as bait to catch fish. (U.S.A. and Africa) **(F)** 2
Squacco Heron Ardeola ralloides	Insects used as bait for catching fish. (Europe) **(F)** 3
Black-breasted Buzzard Gypoictinia melanosternum	Stones dropped to break open Emu (Dromaius novaehollandiae) eggs. (Australia) **(F)** 4
Black Kite Milvus migrans	Smouldering sticks dropped on dry grass in order to feed on small prey flushed out by ensuing fire. (Australia) **(F)** 5
Bald Eagle Haliaeetus leucocephalus	Crickets hit by stones used as missiles and hammers. Also object thrown to attract attention. **F and A** 6
Egyptian Vulture Neophron percnopterus	Aimed throwing of stones to break open Ostrich (Struthio camelus) eggs. (Africa) **(F)** 7
Black Eagle Aquila verreauxii	Dropping of sticks to deter humans approaching nest. (Africa) **(Def.)** 8
Australian Brush Turkey Alectura lathami	Aimed kicking of sand and other debris towards Lace Monitor (Varanus varius) as defence against it. (Australia) **(Def.)** 9
Sandhill Crane Grus canadensis	Towel used to wipe body after swimming. **BC** 10
Sun Bittern Eurypya helias	Maggots used as bait to catch fish. **F** 11
Oystercatcher Haematopus ostralegus	Small stick inserted in cracks on ground in order to goad insects out. **F** 12
Kea Nestor notabilis	Tin used to bale water out of water tray. **P** 13
Palm Cockatoo Probosciger aterrimus	Leaf used to prevent a nut slipping in the mouth when attempting to crack it. (Australia) **(F)** 14

Table 8.1 (continued)

Greater Sulphur-crested Cockatoo Cacatua galerita	Stone used to scrape earth away. P 15
Lesser Sulphur-crested Cockatoo Cacatua sulphurea	Various objects used as aids in grooming. Also objects used for holding drinking water. **BC and Dr.** 16
Bare-eyed Cockatoo Cacatua sanguinea	Matchstick used to scratch parts of body not normally reachable. **BC** 17
Moluccan Cockatoo Cacatua moluccensis	Various objects used to scratch body. **BC** 18
"Cockatoo" Cacatua spp.	Nut shells used to hold water for drinking. **Dr.** 19
Blue-fronted Amazon Parrot Amazona aestiva	Chewing stick used to groom head feathers. **BC** 20
Yellow-fronted Amazon Parrot Amazona ochrocephala	Toy bell used as food scoop. F 21
African Grey Parrot Psittacus erithacus	Objects used to scratch back and neck feathers. Briar pipe used to bale water from water bowl. **BC and P** 22
Eclectus Parrot Eclectus roratus	Palm frond used in excavating nest burrow. **NB** 23
Striped Owl Rhinoptynx clamator	Leaves used to wipe blood from body of offspring. **BC** 24
Pied Kingfisher Ceryle rudis	Bread used as bait to catch fish. (Africa) **(F)** 25
Australian Bee-eater Merops ornatus	Stick used when digging nest burrow. (Australia) **(NB)** 26
Gila Woodpecker Centurus uropygialis	Pieces of bark and seeds coated with honey as method of feeding the honey to offspring. (U.S.A.) **(F)** 27
Blackbird Turdus merula	Twig used to clear snow from ground when foraging. (Europe) **(F)** 28
American Robin Turdus migratorius	Twig used to clear leaf litter from ground when foraging. (U.S.A.) **(F)** 29
Pekin Robin Leiothrix lutea	Vine shoots and pieces of leaves used in body care. **BC** 30
Eastern Shrike-tit Falcunculus frontatus	Twig used to dislodge invertebrate from crevice in tree branch. (Australia) **(F)** 31
Grey Thrush Colluricincla harmonica	Twig used to goad insect from hole in a brick. (Australia) **(F)** 32

Table 8.1 (continued)

Blue Tit Parus caeruleus	Twig used to dislodge nut from food hopper. (Europe) **(F)** 33
Mountain Chickadee Parus gambeli	Splinter probed in crack in tree. (U.S.A.) **(F)** 34
Orange-winged Sittella Neositta chrysoptera	Twigs used to probe for grubs in tree-holes. (Australia) **(F)** 35
Brown-headed Nuthatch Sitta pusilla	Pieces of bark used to lever off other pieces of bark so exposing insect prey. (U.S.A.) **(F)** 36
White-breasted Nuthatch Sitta carolinensis	Application of crushed beetles to nest cavity opening possibly to deter tree squirrels from entering. (U.S.A.) **(Def.)** 37
Galapagos Ground Finch Geospiza fuliginosa or fortis	As Galapagos Woodpecker Finch. (Galapagos) **(F)** 38
Galapagos Black Finch Geospiza conirostris	As Galapagos Woodpecker Finch. **F** 39
Galapagos Woodpecker Finch Cactospiza pallida	Cactus spine and twigs used to dislodge insect prey from tree bark. (Galapagos) **(F)** 40
Galapagos Mangrove Finch Cactospiza heliobates	As Galapagos Woodpecker Finch. (Galapagos) **(F)** 41
Galapagos Warbler Finch Certhidea olivacea	As Galapagos Woodpecker Finch. (Galapagos) **(F)** 42
White-winged Chough Corcorax melanorhamphus	Mussel (Velesunio ambiguus) shells thrown at and used as hammers on live mussels to break them open. (Australia) **(F)** 43
Satin Bower-bird Ptilonorhynchus violaceus	Wad of bark used as an aid in painting bower. (Australia) **(NB)** 44
Northern Blue Jay Cyanocitta cristata	Pieces of paper used to reach food outside cage. Also paper used to soak up small pieces of food for ingestion. **F and F** 45
Green Jay Cyanocorax yncas	Twigs inserted under bark to capture insects. (U.S.A.) (F) 46
New Caledonian Crow Corvus moneduloides	Twig probed in bark possibly to dislodge insects. (Oceania) **(F)** 47
Rook Corvus frugilegus	Plug inserted in plug-hole preventing escape of water to be used for bathing. **Bath.** 48

Table 8.1 (continued)

Common Crow Corvus brachyrhynchos	Stones used to hammer open acorns. Also innovative use of several small objects to facilitate operation of feeding apparatus in captive situation. (U.S.A.) **(F) and F** 49
Northwestern Crow Corvus caurinus	Stick used to prize peanut from crack. F 50
Fish Crow Corvus ossifragus	Grass dropped on Laughing Gull (Larus atricilla) in apparent attempt to displace it from its nest. (U.S.A.) **(F)** 51
Raven Corvus corax	Rocks thrown at human intruders to deter them from approaching. Also grass dropped on Kittiwake (Rissa tridactyla) to displace it from its nest. (U.S.A.) **(Def.) and (F)** 52

Sources

1. Meyerriecks (1972) 2. Lovell (1957), Shrives (1967), Sisson (1974), Norris (1975), Keenan (1981) 3. Prytherch (1980) 4. Chisholm (1954) 5. Lockwood (1966) 6. van Lawick-Goodall (1970) 7. van Lawick-Goodall & van Lawick-Goodall (1966) 8. Dick & Fenton (1979) 9. Dow (1978) 10. Bartlett & Bartlett (1973) 11. Alder (1974) 12. Olney (1978) 13. Porter (1936) 14. Wallace (1869) 15. Kawata (1974) 16. Smith (1971) 17. Smith (1970) 18. Boswall (1983) 19. Fyleman (1936) 20. Blanden (1977) 21. Murphy (1978) 22. Smith (1971), Kruijt (1974), Taylor (1975), Janzen et al (1976) 23. DeCourcey (1978) 24. Goodman & Fisk (1973) 25. Root (1978), Douthwaite (1979) 26. Chisholm (1954) 27. Antevs (1948) 28. Priddey (1977) 29. Potter (1970) 30. Gibson (1978) 31. Richards (1971) 32. Mitchell (1972) 33. Coombes (1974) 34. Gaddis (1981) 35. Green (1972) 36. Morse (1968) 37. Kilham (1971) 38. Hundley (1963) 39. Millikan & Bowman (1967) 40. Lack (1947), Millikan & Bowman (1967) 41. Curio & Kramer (1964) 42. Hundley (1963) 43. MacDonald (1970), Hobbs (1971) 44. Gannon (1930) 45. Jones & Kamil (1973), Judd (1975) 46. Gayou (1982) 47. Orenstein (1972) 48. see chapter 9 49. Powell & Kelly (1977), Duvall (1978) 50. Jewett (1924) 51. Montevecchi (1978) 52. Janes (1976), Montevecchi (1978).

Table 8.2. List of tool-using bird species and details of their life history/ecology. Feeding habitat is broadly categorized as water (W), terrestrial (T), aerial (Ae) or arboreal (A). Main type(s) of diet are: P - piscivorous; I - insectivorous (includes other invertebrates); F - frugivorous; G - granivorous; H - herbivorous; C - carnivorous; O - omnivorous. Mainland/island entries refer to species as a whole and not necessarily to tool-using individuals. Data from original sources and also from Walters (1980).

	Captive/ Wild	Nidicolous/ Nidifugous	Passerine/ Non-passerine	Feeding habitat	Diet	Mainland/ Island
Double-crested Cormorant	W	NC	NP	W	P	M
Green Heron	W	NC	NP	W	P	M
Squacco Heron	W	NC	NP	W	IP	M
Black-breasted Buzzard	W	NC	NP	T	C	I
Black Kite	W	NC	NP	T	O	M
Bald Eagle	C	NC	NP	T	C	M
Egyptian Vulture	W	NC	NP	T	C	M
Black Eagle	W	NC	NP	T	C	M
Australian Brush Turkey	W	NF	NP	T	FI	I
Sandhill Crane	C	NF	NP	T	O	M
Sun Bittern	C	NC	NP	W	P	M
Oystercatcher	C	NF	NP	T	I	I
Kea	C	NC	NP	T	O	I
Palm Cockatoo	W	NC	NP	A	F	I
Greater Sulphur-crested Cockatoo	C	NC	NP	A	F	I
Lesser Sulphur-crested Cockatoo	C	NC	NP	A	F	I
Bare-eyed Cockatoo	C	NC	NP	A	F	I
Moluccan Cockatoo	C	NC	NP	A	F	I
"Cockatoo"	C	NC	NP	A	F	I
Blue-fronted Amazon Parrot	C	NC	NP	A	F	M
Yellow-fronted Amazon Parrot	C	NC	NP	A	F	M
African Grey Parrot	C	NC	NP	A	F	M
Eclectus Parrot	C	NC	NP	A	F	I
Striped Owl	C	NC	NP	T	C	M
Pied Kingfisher	W	NC	NP	W	PI	M
Australian Bee-eater	W	NC	NP	Ae	I	I
Gila Woodpecker	W	NC	NP	A	O	M
Blackbird	W	NC	P	T	IF	M
American Robin	W	NC	P	T	IF	M
Pekin Robin	C	NC	P	T	IGF	M
Eastern Shrike-tit	W	NC	P	T	I	I
Grey Thrush	W	NC	P	T	IC	I
Blue Tit	W	NC	P	A	IGF	I
Mountain Chickadee	W	NC	P	A	I	M
Orange-winged Sittella	W	NC	P	A	I	I
Brown-headed Nuthatch	W	NC	P	A	IG	M
White-breasted Nuthatch	W	NC	P	A	IF	M
Galapagos Ground Finch	W	NC	P	T	GI	I
Galapagos Black Finch	C	NC	P	T	GI	I
Galapagos Woodpecker Finch	WC	NC	P	A	I	I

Table 8.2 (continued)

Galapagos Mangrove Finch	W	NC	P	A	IH	I
Galapagos Warbler Finch	W	NC	P	A	I	I
White-winged Chough	W	NC	P	T	ICG	I
Satin Bower-bird	W	NC	P	A	FI	I
Northern Blue Jay	C	NC	P	T	O	M
Green Jay	W	NC	P	T	O	M
New Caledonian Crow	W	NC	P	T	O	I
Rook	C	NC	P	T	O	I
Common Crow	WC	NC	P	T	O	M
Northwestern Crow	C	NC	P	T	O	M
Fish Crow	W	NC	P	T	O	M
Raven	W	NC	P	T	O	M

Chapter 9. Tool-use by a captive rook and its causation*

INTRODUCTION

One reason for studying animal tool-use is that it may tell us something about the behavioural plasticity of the species using the tool. Although all cases of tool-use cannot be viewed as being behaviourally homologous (Hall 1963), they are in some way analagous with each other. This may enable us to draw useful comparisons across species, including our own, regarding the necessary and sufficient conditions under which these behaviours originated. Alcock (1972) defined tool-use as involving ".....the manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal's efficiency in altering the position or form of some separate object." In his book on the subject Beck (1980), to reiterate, gave a more exacting, but verbose, definition, stating that "tool-use is the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool." By implication a resource (in the word's widest sense), or resources, not normally available to the tool-user becomes available. A somewhat different, more formal, approach to that of Boswall (1977,1978, 1979, 1981, 1983) was adopted in the review of the subject which precedes this chapter.

* Published reports of this study are to be found in Reid (1980, 1982).

Apart from humans, tool-use is rare in the animal kingdom, and only a few species use tools regularly, e.g. the chimpanzee, Pan troglodytes (van Lawick-Goodall 1970), the California sea otter, Enhydra lutris (Hall and Schaller 1964), the Galapagos woodpecker finch, Cactospiza pallida (Lack 1947a), the solitary wasp, Ammophila urnaria (Peckham and Peckham 1905). That it is rare, both in terms of the small number of species exhibiting it and also with respect to its generally low frequency of occurrence within a species, suggests that animals generally are well-adapted, both behaviourally and morphologically, to their respective habitats and do not require the use of implements in order to survive. This rarity also makes it difficult to conduct intensive studies, especially under unpredictable conditions in the field.

This chapter describes an example of tool-use by a young captive rook, and investigates the role played by some factors involved in its causation.

The Birds

From 10 August 1976 until 28 July 1978 one juvenile and three adult rooks lived in an aviary in the town of St. Andrews, Fife. Two of the adults, a male and a female, were over 10 years of age, and the other adult was over three years of age. These birds had spent most of their lives in captivity. The juvenile bird was hatched in another aviary in April, 1976, and was an offspring of the two old rooks. All the birds fed ad libitum on game chick starter pellets, supplemented every three or four days with mealworms, Tenebrio molitor, and occasionally with raw meat and household leftovers. They also captured small invertebrates which ventured into the aviary. Every time I visited the aviary I gave the birds

fresh drinking and bathing water.

The Aviary

Figure 9.1 (p. 305) shows a plan of the aviary, which is situated in a secluded garden frequented by few people. It is 4.8m long and 3.2m broad, except for one part which is only 2.4m broad, and 2.25m high. Three walls consist of wire mesh with copper gauze on the interior, restricting the rooks' view of the outside world and thus preventing undue disturbance. The north wall is made of wood. The roof consists of wire mesh and copper gauze, but a 1m wide wooden strip along the north side provides shelter for the birds. Two panels of copper gauze divide the interior of the aviary into three inter-connecting sections. The south quarter of each section is 0.33m deeper than the rest of the section, thus making three (1.6 x 0.8 x 0.33) m^3 sinks. The floor ($14m^2$) of the aviary is cement, and the total aviary space is approximately $33m^3$.

Branches and bits of wood, as well as wooden ledges, provided perches in the aviary, and twigs and sticks were present, but the birds never attempted to build a nest. Various nooks and crevices existed, some made by the rooks pecking at the walls and other parts of the structure.

In order that rain water could drain away, the aviary was designed with a plug-hole (a "top" hole), 4.5cm in diameter, at the south end of each section on the floor, which is on a slight incline. There is also one plug-hole in each sink (a "bottom" hole), making a total of six holes in the aviary. Overflowing from adjoining aquaria, waste water containing little organic material, continuously seeped under the north wall in the east section, and drained away down the top hole there. Only once during this study, for 12 days,

did this water source flow into the middle section. Waste water never flowed into the west section. All the birds drank from the top hole in the east section.

When the rooks were initially introduced to the aviary there was one plug, 4.5cm tapering to 4cm in diameter, and 1cm thick, present. This plug size is the correct one for insertion into the plug-holes to prevent water draining away.

INITIAL OBSERVATIONS

On 14 July 1977, before giving the birds fresh water, I found the plug perfectly positioned in the top hole of the east section. This had flooded the section with a pool of water about 2.5m in area and 1.5cm deep, which flowed over the small (1.5 cm high) curb into the sink and drained away via the bottom hole there. I removed the plug and left it near the hole. Two days later I again found the plug positioned in the hole with the resulting pool of water. Over the next seven days I discovered the plug in the hole on a further four occasions. During this period, I watched the rooks from a canvas hide erected outside the aviary, and observed the young bird to pick up the plug between the tips of its mandibles (using the metal ring attached to the top of the plug), carry it to the plug-hole and drop it straight into the hole. It then secured the plug with four sharp taps of its bill, making four distinctive sounding, hollow "popping" noises in the process. Despite the skill required to place the plug exactly in the hole, the young rook made the act look very simple. The sound of water draining away ceased at once, and the young bird was immediately joined from the middle section by the three year old rook. This bird began drinking from the area around the plug, while

the young rook visually investigated the bottom hole, in the sink of the section. Both rooks left the section 2min later.

At that time of year the birds were in moult, and suggestive evidence that they were using the pool of water for bathing comes from the fact that I found moulted feathers there on days of, and just after, the occurrence of plug-inserting behaviour. Normally, I saw few signs of use of the east section such as faeces, pellets, etc.

This performance by the young rook meets Alcock's (1972) and Beck's (1980) criteria in the strictest sense, and thus qualifies as tool-use.

FURTHER OBSERVATIONS

Methods

Selectivity of plug-moving. In order to resolve whether, or not, the young rook (and possibly the other birds) merely moved plugs in a random manner, or were selective about where to move them, I introduced a further five plugs into the aviary on 9 August 1977. Each plug was marked with a number from one to six on the underside. I divided the aviary floor into 22 quadrats, equal in shape and area, and placed one plug in a quadrat near each hole, its home quadrat thereafter (see Fig. 9.1, p. 305). On succeeding visits to the aviary I recorded the new plug positions with respect to the 22 quadrats, which could only have resulted from plug-moving by the bird(s). A plug-moving was defined as the finding of a plug in a quadrat other than that plug's home quadrat. I also identified two forms of tool-use: attempted tool-use (ATU), a weak form of the behaviour, in which a plug was positioned in a hole such that it

would not prevent, or was not preventing, the drainage of water down that hole; and successful tool-use (STU), a strong form of the behaviour, in which a plug was inserted in a hole such that it would prevent, or was preventing, the drainage of water. If neither had occurred between visits to the aviary the intervening days were scored as being ones of no tool-use (NTU). The time for a section of the aviary to fill up with water and overflow into a sink once a plug had been inserted in one of the top holes was around four hours. Having recorded this information, I returned any plugs that had been moved to their home quadrats and repeated the procedure on the next visit to the aviary.

Availability of water. In order to determine the relationship, if any, between the amount of fresh water available to the rooks and the occurrence of tool- using behaviour, I randomly varied the former with respect to three conditions. I either gave them one large bowl, approximately 60 x 35cm, containing sufficient water for them to bathe in and drink from, or four small bowls, approximately 10cm in diameter and 8cm deep, containing enough water for drinking but not for bathing, or I gave them no water at all. Of course the birds always had available the water source from the aquaria, and they were not subjected to the third condition for more than 23hr. at a time.

Effects of weather. In order to assess any relationship between the weather and the occurrence of tool-using behaviour I obtained various meteorological data from the Geography Department of the University of St. Andrews. These were daily maximum temperature, minimum temperature, mean temperature (taken as the mean of the maximum and minimum temperatures), temperature range (maximum minus minimum temperature), hours of sunshine, relative humidity and rainfall.

Plug-moving records were available for 138 days. Sometimes I had to extrapolate on which day STU had taken place, which meant being, at most, one day out in the estimation of when it had really occurred. I scored ATU as happening on the day I visited the aviary, unless I had reasons for thinking otherwise (e.g. some accumulation of water in a section). These possible inaccuracies make no difference to subsequent analyses, however, as there were no statistically significant differences between days I scored as tool-using ones and the days immediately preceding them (see Table 9.1, p. 301). Data on water conditions were available for all days of the study (N=380), and the meteorological data for almost all of them. I made comparisons on these measures between STU+ATU days against NTU days, and, as a stronger measure of whether tool-use was related to them, also between STU days and ATU+NTU days.

Results

Plug-moving. During the period that six plugs were available to the birds, 477 instances of plug-moving occurred. On 22 different days STU occurred 16 times and ATU 10 times. Figure 9.2 (p. 306) shows the frequencies to which each quadrat had a plug placed in it, as well as the respective frequencies of ATU and STU. Clearly, the distribution is biased, with quadrats 7,8 and 20 receiving plugs more often than the others ($D = 0.21$, $p << 0.002$, Kolmogorov-Smirnov test). Directly above quadrats 7 and 8, 30cm from the aviary roof, there is a hole, 2cm x 20cm, in the copper gauze, caused by the birds' pecking. This hole was a site of the birds' manipulatory play, and I found plugs inserted into it on 21 occasions. The high frequencies of plug-moving to quadrats 7 and 8 are accounted for by unsuccessful attempts at inserting a plug in this hole, plugs falling

into these quadrats with about equal frequency. Even with the data from these two quadrats discounted, the frequency distribution remains significantly biased ($D = 0.26$, $p << 0.002$, Kolmogorov-Smirnov test). Apart from quadrat 20 in the east section, the only other quadrat to receive plugs more often than expected was quadrat 13 in the middle section. This was where water drained away for 12 days during the study, and it was the only other site of STU and ATU.

Water conditions. Table 9.2 (p. 302) shows the number of days STU+ATU versus NTU occurred with respect to the three water conditions, and Table 9.3 (p. 302) shows similar data for STU versus ATU+NTU. There was no relationship between water conditions and the occurrence of the tool-using behaviour in either its weak or strong form.

Weather. Tables 9.4 and 9.5 (pp. 303 and 304) show the results of the analysis regarding days of STU,ATU and NTU and the meteorological conditions on these days. In its weak form (STU+ATU) tool-use tended to occur on drier days, i.e. those of significantly lower relative humidity and lower rainfall (Table 9.4, p. 303). These two measures are correlated on STU+ATU days, but with the effects of temperature partialled out they do not covary ($r = 0.29$, 20 df, $p > 0.1$). The stronger form (STU only) of the behaviour occurred on days of even lower relative humidity, lower rainfall and higher maximum temperatures (Table 9.5, p. 304). These three measures are inter-correlated on STU days. Maximum temperature and relative humidity do not covary with rainfall partialled out ($r = 0.38$, 12 df, $p > 0.1$). However, both humidity and maximum temperature covary with rainfall, even with the effects of the other partialled out ($r =$

0.60, 12 df, $p < 0.05$ and $r = -0.78$, 12 df, $p = 0.001$ respectively). This means that STU tended to occur on days which were both drier and warmer than other days.

DISCUSSION

These observations demonstrate that the bird, or birds, moving the plugs did so selectively, and that the tool-using behaviour was focussed on the water trickle. In its weaker form, tool-use was performed on drier days, and in its stronger form on both hotter and drier days. Other aspects of the weather were comparatively unimportant in its elicitation, and neither was the amount of fresh water available to the birds important. It seems reasonable to equate the weaker form of tool-using behaviour with moderate strength of motivation to use the tool, and the strong form of tool-use with strong motivation to use it. Given the apparent ease with which the young rook used the tool, this seems justified. This means, then, that on dry days the young rook (or possibly another bird) had moderate motivation strength to insert the plug into the appropriate hole, while if those days were also warm ones then the bird was strongly motivated to tool-use.

Of the 50 or so bird species now known to have used tools (see chapter 8), eight are members of the family Corvidae (Northwestern crow, Corvus caurinus, Jewett 1924; New Caledonian crow, C. moneduloides, Orenstein 1972; Northern blue jay, Cyanocitta cristata, Jones & Kamil 1973; raven, C. corax, Janes 1976; common crow, C. brachyrhynchos, Powell & Kelly 1977; fish crow, C. ossifragus, Montevecchi 1978; green jay, Cyanocorax yncas, Gayou 1982; and the present example). Of these, six are members of the

genus Corvus, which has more tool-using species than any other in the animal kingdom. This is not surprising since corvids are well-known to be inquisitive and playful birds (Wilson 1975, p. 166), and the importance of such attributes in the development of tool-using has been stressed by Hall & Schaller (1964) and Alcock (1972). Play and exploration facilitate the incorporation of new behaviours into an individual's repertoire and eventually a species' ethogram, provided they are sufficiently rewarding in terms of economy of energy expended, or an increase in resources made available (see e.g. Hinde & Fisher 1952). The fact that in this study the one rook known to be a tool-user was a young bird serves to underline the importance of play - young animals in general being more playful than adults. This particular bird was especially adept at manipulating its food, often inserting mealworms into small holes in the aviary structure only to retrieve them from the opposite end again. I did not observe this behaviour in its companions. The high rates of plug-moving in this study also illustrate that rooks are extremely explorative and playful. Note especially the high frequency of plug-moving to quadrats 7 and 8 resulting from behaviour with little obvious purpose other than play.

The young rook apparently perceived the relationship between plug-hole and plug, and, when appropriate weather conditions prevailed, it performed the appropriate motor response. One possible explanation of the origin of the behaviour is that the plug may have been knocked into the hole fortuitously by a bird looking for food. Foraging rooks in the wild often flick over stones, small piles of loose turf, etc. with a swift lateral movement of the bill, so exposing hidden invertebrates on which to feed (personal observation). I have observed the captive birds so flicking plugs. If the original plug in the aviary was sufficiently close to the hole

in quadrat 20, and was flicked aside by a foraging rook, it may, by chance, have landed in the plug-hole. As water accumulated, the relationship between plug, plug-hole and the resulting pool of water may have been perceived by the young rook. Alternatively, the bird may have perceived this relationship through playing with the plug, or it may have been a case of insightful discovery. The most likely explanation, however, is that the tool-using behaviour was acquired through normal food-hiding behaviour. The birds in the present study regularly hid mealworms in corners and holes in the aviary, and hoarding behaviour is well documented for wild rooks (Purchas 1975, Kallander 1978). A plug-hole would seem to present an ideal place for hiding food items, and a plug an equally ideal object for concealing the cache. Once performed, the act of plug-insertion would be reinforced by the formation of the pool of water, possibly via secondary reinforcement of the cessation of the noise of water draining away.

What are the environmental factors leading to tool-use in this case? Tool-use by other animals usually involves the attainment of a resource when there is some barrier present which prevents an individual exploiting that resource using its normal behavioural or morphological adaptations. Such environmental barriers are more likely to be present in the restricted conditions of captivity (see chapter 8). A key resource here seems to be bathing water. Prior to this study the captive rooks bathed daily. Although the large bowl of water, (which contained the maximum amount of water given to them), was large enough for one rook at a time to bathe in, it was not capable of holding more than one at a time, and there may not even have been enough water for four rooks to have a daily bath, since bathing involves spillage. The environmental barrier in this example of animal tool-use appears to have been a shortage of bathing

water. The effect of this barrier seems to have been increased motivation to use the plug when the weather was warm and dry. Though little is known of the exact causation of bathing behaviour in birds, it seems likely that in warm, dry weather they bathe more often than usual, if not to remove formerly wet, foreign matter sticking to their plumage (and so facilitate preening), then perhaps to cool themselves. Mes et al (1978) in fact found that common terns, Sterna hirundo, in Holland, attempted to cool themselves on a hot day by skimming the water with their bills.

In conclusion, I suggest that too little stress has been placed on the role of mediating processes in discussions of animal tool-use. Even if they are not invoked by the organism it would seem justifiable to categorise tool-using and other similar behaviours (e.g. snail-smashing by song thrushes Turdus philomelos) according to their complexity, by defining what cognitive abilities the animal would seem to have in order to perform such acts. Although all tool-using acts are not behaviourally homologous (Hall 1963), they are roughly similar ecologically. The pressures on animals to use tools are in some cases analogous to one another, in that they arise because of some thwarting influence in the environment, which prevents access to resources. The effect of these analogous pressures are of interest phylogenetically in demonstrating how different animals solve similar problems, and illustrating how comparatively complex their solutions are.

Table 9.1. Mean values of the various weather data on days of tool-use and the days immediately preceding them. All t scores are non-significant.

(a) ALL TOOL-USE DAYS (ATU+STU)

		MEANS	
		TU DAYS	TU DAYS -1
MAXIMUM TEMPERATURE	F=1.22, t=0.72, 42df	13.05	14.19
MINIMUM TEMPERATURE	F=1.18, t=0.53, 42df	7.04	7.68
MEAN TEMPERATURE	F=1.24, t=0.66, 42df	10.05	10.94
TEMPERATURE RANGE	F=1.04, t=0.40, 42df	5.95	6.30
SUNSHINE	F=1.05, t=0.25, 42df	3.62	3.96
HUMIDITY	F=1.31, t=0.22, 42df	68.50	69.45
RAINFALL	F=3.74, t=0.99, 42df	0.76	1.31 *

* t-test when variances differ

(b) STU ONLY DAYS

		MEANS	
		STU DAYS	STU DAYS -1
MAXIMUM TEMPERATURE	F=1.37, t=0.41, 26df	14.67	15.46
MINIMUM TEMPERATURE	F=1.63, t=0.36, 26df	7.89	8.49
MEAN TEMPERATURE	F=1.60, t=0.40, 26df	11.28	11.97
TEMPERATURE RANGE	F=1.73, t=0.15, 26df	6.78	6.64
SUNSHINE	F=1.25, t=0.26, 26df	3.90	3.46
HUMIDITY	F=1.08, t=0.82, 26df	63.43	67.29
RAINFALL	F=2.92, t=1.05, 26df	0.70	1.37 *

* t-test when variances differ

Table 9.2. Water conditions on days of weak (ATU+STU) tool-use and days of no tool-use (NTU).

	WATER CONDITION		
	Large Bowl	Small Bowls	No Water
DAYS OF ATU+STU	12	9	1
DAYS OF NTU	209	101	48

X^2=2.47, 2df, P=0.30

Table 9.3. Water conditions on days of strong tool-use (STU) and and other days (ATU+NTU).

	WATER CONDITION	
	Large Bowl	Small Bowls/No Water
DAYS OF STU	12	2
DAYS OF ATU+NTU	209	157

X^2=3.44, 1df, P=0.06

Data for Small Bowls and No Water conditions have been pooled.

Table 9.4. Means ± standard deviations of meteorological measures on days of tool-use in its weak form (ATU+STU) compared with similar data for days of NTU.

	ATU+STU	NTU	t	df	P
Minimum temperature (^{o}C)	7.04±4.18	5.93±5.00	1.02	370	0.31
Maximum temperature (^{o}C)	13.05±5.52	11.35±5.78	1.34	366	0.18
Mean temperature (^{o}C)	10.05±4.69	8.70±5.24	1.18	365	0.24
Temperature range (C^{o})	5.95±2.86	5.37±2.75	0.94	365	0.65
Sunshine (hr)	3.62±4.19	2.67±3.76	1.15	377	0.25
Humidity (%)	68.50±14.93	75.87±12.11	2.73	367	0.007*
Rainfall (mm)	0.76±1.19	1.98±5.15	3.24	378	<0.005*

t-tests for independent means, all variances equal except those for rainfall.

*Indicates statistical significance.

Table 9.5. Means ± standard deviations of meteorological measures on days of tool-Use in its strong form (STU) compared with similar data for all other days (ATU+NTU).

	STU	ATU+NTU	t	df	P
Minimum temperature (^{O}C)	7.89±4.82	5.92±4.95	1.46	370	0.14
Maximum temperature (^{O}C)	14.67±5.49	11.33±5.76	2.14	366	0.03*
Mean temperature (^{O}C)	11.28±5.05	8.68±5.20	1.83	365	0.07
Temperature range (C^{O})	6.78±2.23	5.35±2.76	1.90	365	0.06
Sunshine (hr)	3.90±4.84	2.68±3.74	1.18	377	0.24
Humidity (%)	63.43±12.70	75.90±12.16	3.76	367	0.0002*
Rainfall (mm)	0.70±1.22	1.95±5.10	2.90	378	<0.01*

t-tests for independent means, all variances equal except those for rainfall.

*Indicates statistical significance.

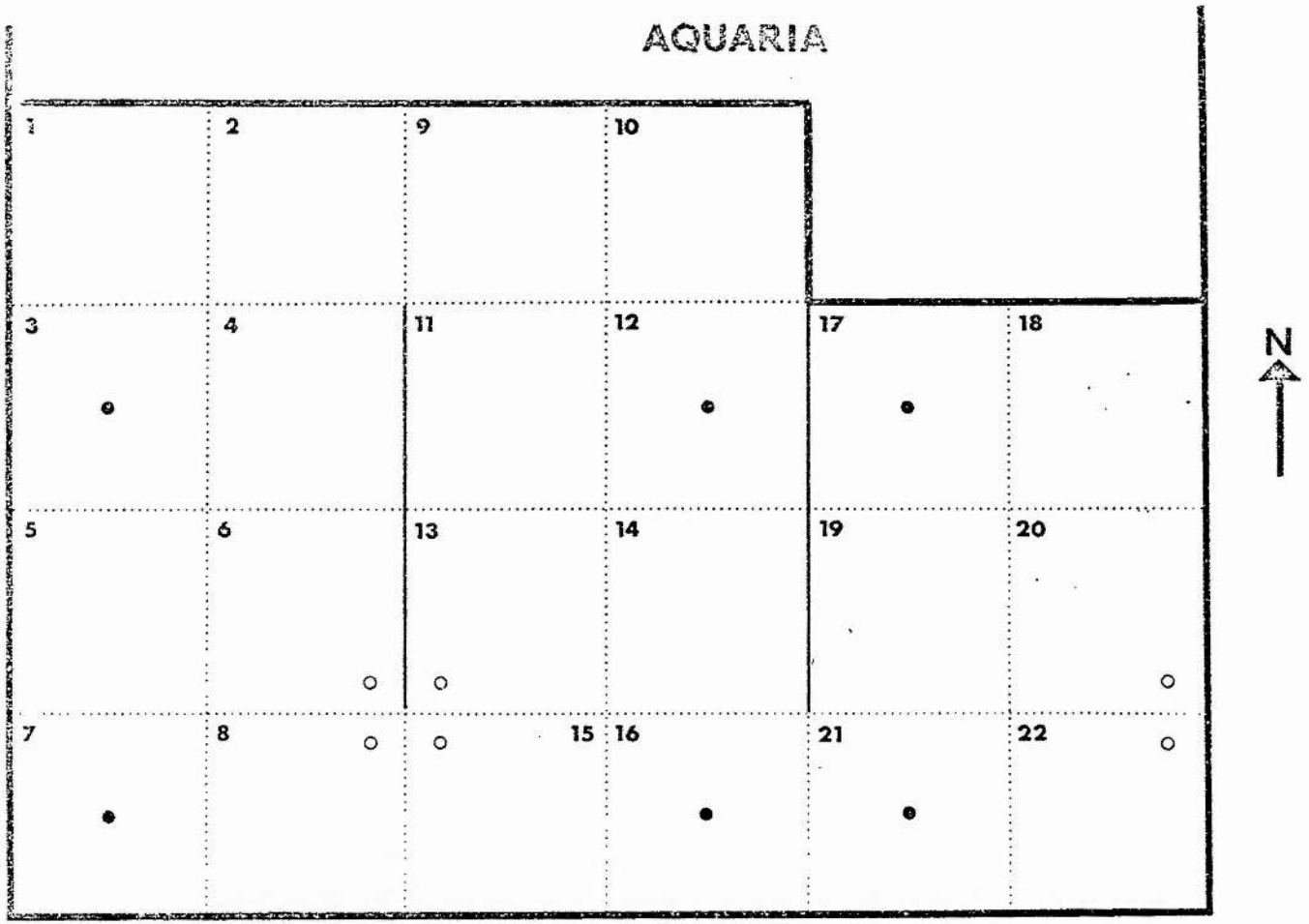


Figure 9.1 Plan of the aviary showing 22 quadrats with plug-holes (o), and plugs (•) in their home quadrats. The solid lines within the aviary perimeter represent copper gauze panels. There are also low dividing walls between quadrats 2 and 9, 8 and 15 and 16 and 21.

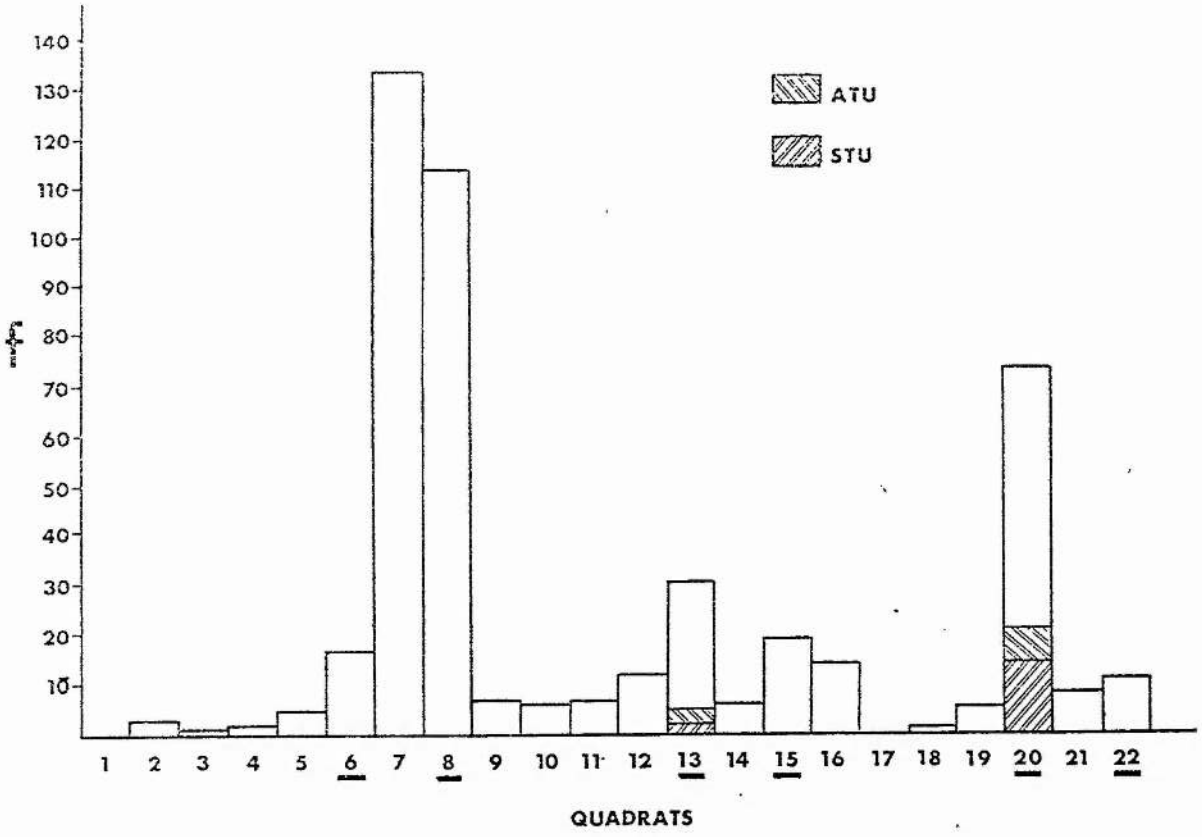


Figure 9.2 Frequencies of plug-moving to all quadrats, and of STU and ATU. Quadrat numbers underlined mean that that quadrat has a plug-hole in it.

Chapter 10. Conclusions

Some of the major results of the research reported in this thesis may be summarised as follows:

1) The large decline of the British rook population that took place from around the 1940's was almost certainly due to the changes in national policy that has made agriculture one of the largest industries in Britain today. The changes and innovations directly responsible for reduced numbers of breeding rooks were probably the introduction of harmful pesticides and, perhaps more obviously, changes in land use and methods of cultivating the land. Of particular significance were the ploughing up of old grassland and a swing to barley as the major cereal crop.

2) North-east Fife is similar to many other agricultural regions of Britain in that it was not exempt from these changes and the concomitant decrease in rook numbers.

3) Rook population size in a particular year in N.E. Fife was better predicted by the pattern of land use two years earlier as opposed to the pattern in that year itself, suggesting that many young birds were not surviving to breed at the normal age of two years.

4) The young which did survive to breed founded or adopted rookeries in which to do so in such a manner as to produce a clumped distribution of smaller rookeries (with larger rookeries being relatively isolated) in the 1970's.

5) Rookery attendance by rooks was greatest during the breeding season and feeding flock sizes were largest in the evenings (i.e. after 1800 hr G.M.T.) and in autumn/winter.

6) Throughout the year rooks generally foraged on grass more than any other type of field, but fields which contained exploitable barley grain were preferred when they were available. Ploughed

fields were also important feeding stations for rooks.

7) Carrion crows also utilised grass fields to a large degree, but stubble fields were less important to them. They foraged often on mudflats and preferred dung (heaps and covered fields) more than did rooks.

8) Rooks and carrion crows overlapped greatly in their use of the habitat and used some field types to a disproportionately greater degree than would be expected from the abundance of these field types.

9) The rook appeared to be more of a generalist than the carrion crow with regard to its habitat choice.

10) When niche overlap was high between the two species then the carrion crow narrowed its niche to a greater extent than did the rook. This may be seen as a carrion crow strategy to avoid direct competition with large flocks of rooks.

11) In captivity, individual rooks were subordinate to individual carrion crows, but patterns of dominance amongst all captive birds did not reflect priority of access to food.

12) The diet of young rooks was found to be predominantly composed of barley, while the invertebrate part of it was mainly comprised of beetles, tipulids and snails.

13) Examples of avian tool-use are generally confined to performances by individuals who are faced with barriers which prevent goals being attained by normal means.

14) A young, captive rook, thwarted by a lack of bathing water, used a tool (plug) in order to prevent water draining away so that a bathing pool would form on its aviary floor. The bird did this on days which were, on average, significantly warmer and drier than other days.

Apart from these and other specific results of this

research, one major aspect of rook biology has emerged clearly. This is that the rook is an extremely adaptable bird. This is true both in an ecological and a behavioural sense. That the rook is adaptable and successful as a species was well-known previously, of course. Several facets of its natural history testify to this, such as its wide distribution in Europe and Asia, its very high population density in some parts of its range resulting in massive colonies while occasionally nesting in single pairs, its ability to migrate over long distances, the current evidence that it is recovering after large scale population decline and even spreading northwards and, in broad terms, its role as a generalist in ecological communities. The findings of this investigation confirm and extend this view of the rook as a species which displays ecological and behavioural plasticity. Behavioural adaptability is well revealed by its potential for innovative use of objects, such as that reported in chapter 9. The young rook was the only bird seen tool-using but the others in the aviary could also have done so. Some weeks after the tool-use study ended (weeks of no further tool-use) the young rook was removed from the aviary. Two carrion crows, the subjects of study in chapter 7, were then placed in the aviary to accompany the remaining rooks. Several days later a plug was again found perfectly placed in the plug hole of quadrat 20. No further tool-using instances were recorded after this and it is not known whether a rook or a carrion crow was responsible for this final demonstration of plugging behaviour. Attention was drawn in chapters 8 and 9 to the playful propensities of corvids - a fact which enhances, or perhaps governs, the degree of adaptability that this group possesses. Play may be considered to be an activity through which (young) animals acquire experience, practice or skills which help in adopting strategies for dealing with the specific problems to be faced in the

environment. If so, then the varied nature of corvid play and exploration, and the range of contexts in which they appear, are good indicators that these species are ecologically more generalist than many other birds. The few recorded instances of play in birds other than crows tend to be structurally similar to movements performed as components of appetitive behaviours, such as foraging or hunting.

Examples of rook ecological adaptability (still a consequence of the behaviour of individual birds) include the use of a wide range of tree species in which to nest. In this respect they appear to use whichever trees are available. Rooks have also been observed nesting on pylons and chimney ladders (Sage & Vernon 1978) and on the ground (Scott 1959). They have even bred in captivity (Richards 1976). Similarly, rooks are able to exploit a wide variety of food types and parts of their habitat in which to do so. The results of this investigation and of previous ones have shown this. Although earthworms are a major component of the bird's diet none were recorded in the gizzards analysed here. If none were, in fact, given to the young they nevertheless received a variety of other invertebrates. Lockie (1955, 1959) also showed that when earthworms were scarce rooks were able to exploit alternative sources of protein in the breeding season, although breeding was not as successful as when earthworms were more abundant.

The rook is dependent on agriculture and within this constraint is able to find food in a variety of field types (this study, Feare et al 1974, Feare 1978). Grassland is particularly heavily utilised and so are stubble fields, but there is evidence showing that they use most resource stations present more or less in proportion to their abundance. The availability of different field types varies from month to month in accordance with farming strategies and the rook can adapt to this. The large differences in

farming schedules (as well as differences in crop types grown) between the east coast of Scotland (Aberdeenshire, Fife) and Hampshire show even more clearly that the rook's success is not dependent on predictable and stable ecological conditions. As they do use a broad range of resource stations according to their availability then the frequency with which they move from one to another will be high in relation to a species which confines its use of resource stations to a smaller number. This shows that the rook's environment is relatively fine-grained (Vandermeer 1972), and such fine-grained behaviour with regard to field types is matched also by its behaviour within fields, where there is a tendency to move towards certain parts of a field (Waite 1981). Specifically, these are likely to be patches where food abundance is high.

An important aspect of rook biology which promotes the success of this adaptable behaviour is sociality. One proposed function of sociality is that it enables individuals of a species to exploit unpredictably or patchily distributed food sources. One important element in rook diet is earthworms, and these do seem to be spatially and temporally unpredictable in their availability. Rooks are nevertheless able to exploit them via one social mechanism, viz. local enhancement (Waite 1981), which a less social species would be less capable of doing. As pointed out in chapter 3 rooks may also lead a social existence in order that the rookery or roost be used as an information-centre for food finding (Ward & Zahavi 1973). If this is not an evolutionary function of colonial breeding then it is probably a consequence of it. Another benefit of gregariousness that might accrue to individual rooks is that they have a greater likelihood of detecting and avoiding predators. Social life also means that there will be much opportunity for learning from companions. It is not only behaviours which are part of the species

usual ethogram that may be learned and perfected via social facilitation, imitation, observational learning, etc., but also unusual or novel behaviours which might assist in adapting to severe or abnormal environmental conditions. This, in fact, is a clear benefit to individual organisms of behavioural plasticity in general - that it is essential for swift adoption of effective strategies for survival in an unpredictable environment. One may speak here of the evolutionary function of behavioural plasticity as being to allow such short term adjustment. Adaptability at the species level, what I have called ecological adaptability, may be seen as a longer term (spanning generations) strategy for coping with unpredictable fluctuation in environmental conditions, but one which nevertheless can be framed in terms of benefit at the individual level. The consequence of ecological adaptability is that the species survives, and it probably relies more directly on genetic variation, maintained by sexual reproduction, both within and between populations. The benefit to any one individual should accrue via the survival of copies of its own genes in its descendants. The degree of behavioural plasticity shown by individuals in a population will also, of course, depend on genetic variation, but this certainly allows more immediate decisions concerning survival to be made.

As the rook is a bird of generally high latitudes and temperate environments it encounters relatively more patchy ecological conditions than the more stable, predictable ones which prevail in tropical regions (see e.g. Owen 1977). This is well seen with respect to the annual and seasonal variations in its food supply in addition to, and to some extent consequent upon, the spatial and temporal unpredictability (to the rook) of human strategies of land use. It should be of no surprise, then that the rook is such an adaptable generalist. (Interestingly, Partridge (1978) drew

attention to the analogy between the tropical-temperate dichotomy and the mainland-island one, suggesting that island species, like those living in temperate zones, should be more likely to be generalist. If so, this gives further credence to the ideas expressed in chapter 9 regarding island tool-users). But there will also be disadvantages associated with being adaptable and employing generalist policies of exploitation. As a species becomes more specialist in its habits then the number of other species with which it has to compete becomes less. This is true whatever the resource at stake - habitats, food or nest sites. The generalist, however, may have to compete with many other species which also pursue generalist strategies. Certainly, the rook overlaps in its habitat use with many other similarly sized bird species, including other corvids, waders and gulls, and also in its diet (to varying degrees) with these species and also the starling. The potential problems of active or passive competition, at least for the rook in Scotland, may be exacerbated because it is sedentary. The other species which overlap ecologically with it are migratory to different extents and so are able to exploit rook feeding grounds on an opportunistic basis. Although rooks in Scotland may make medium distance movements to exploit food supplies they do not undertake long distance seasonal migration as continental rooks do. Perhaps intraspecific competition is of significance in governing the migratory habits of European rooks, but the reasons for the difference between the two populations could be worth studying closely to see if competition with other species plays an important role.

The nature of the rook's environment once again may be seen as a reason why there may be a greater risk of interspecific competition. The already mentioned unpredictable nature of this makes it a heterogeneous and therefore fine-grained environment

(Vandermeer 1972), and Morse (1971) has shown that in such an environment one should expect strong selection for species which are generalists, and, conversely, selection for specialists in coarse-grained environments. Furthermore, he also argues that species in temperate regions which feed mainly on insects in the summer and seeds in the winter should not evolve extremely specialised morphological characters. This would seem to apply to the rook. Although the rook's bill may be specialised to some degree, in relative terms it is all purpose for the size of the bird, allowing manipulation of insects and seeds of various sizes, as well as some ability for the exploitation of vertebrate foods. Much of the above discussion of adaptability also applies to one of the rook's potential competitors, the carrion crow. In fact the two species certainly do compete, but the extent to which they do so has not been clearly quantified despite this and other studies. When two species compete for a limited resource then a likely outcome of this process is that one species will become more specialist than the other (Krebs 1978). This follows when one considers that if use of one resource by a species makes it less profitable for the other species to exploit then the latter species will reduce its use of that resource, so decreasing its niche breadth, or at least one component of it. (Alternatively, the result could be a shift in the niche by the species compensating for the loss of one resource by exploiting another new one. This would be more likely to happen in young communities, however, because in older, established ones fewer unexploited niches would be available). The species which should reduce its niche breadth will be the one which is less able to defend the resource against the other, i.e. the subordinate one. This need not assume that competition between them will be of the active or contest type as a subordinate species could merely avoid the dominant

one. We can neither know how rooks and carrion crows apportioned themselves parts of the environment nor how ensuing interactions eventually led to the present day situation in N.E. Fife. But as the rook is subordinate to the carrion crow in one to one interactions we should expect it to have narrowed its niche breadth and become more specialised than the carrion crow when the two first began to overlap. As explained in chapter 5 the converse seems to be the case. We return now to sociality as a possible reason why the rook is more generalist than the carrion crow. Chapter 7 showed that subordinate rooks were able, in effect, to increase their competitive ability over dominant carrion crows by being in a group gregariousness, and this also offers a possible mechanism whereby in the historical or evolutionary past rooks did not become more specialist than carrion crows when perhaps we would have expected them to have become so. Much of this, while soundly based, is speculative and obviously a great deal of fruitful research could be undertaken to elucidate the dynamics of niche use by, and competition between, not only these two species but other corvids as well. Most parts of Britain are attractive as study areas since they support five or more species of the family. Comparisons between different localities within Britain (and between British and European communities) might reveal different patterns of ecological interactions dependent upon the number and identity of the congeneric or confamilial species present.

The most successful animal species will be those who are able to adapt to changing conditions, and these are usually and increasingly perpetrated by humans. Species with very narrow ecological requirements, i.e. specialists, will therefore be at risk from the sometimes drastic alteration of their environment. Thus, the survival of species such as the corncrake Crex crex is threatened because the bird seems unable to adapt to the loss of suitable

nesting habitat which has resulted from modern farming methods and other 'improvement' of the land by humans (Cadbury 1980). On the other hand, species with broad ecological preferences, i.e. the generalists such as the rook, the starling and certain gull species, will be less at risk because they are more adaptable. Such species may not only adapt to environmental changes but may become dependent on human activity for survival. This highlights another potential disadvantage of the generalist strategy. Birds which take advantage of increases in resources made possible by humans, such as which happens on farmland, may come into direct conflict with them and so be persecuted. The rook certainly has been. In order that the rook continues to survive, studies such as the present one, which provide the necessary foundation for going on to assess the bird's status as an agricultural pest or ally, should continue to be done. As the landscape is further developed and altered by humans this, indeed, will be essential. For example, as autumn sown barley becomes more popular with farmers it will be necessary to examine the impact rooks have on this. They will not be slow to exploit it if it proves efficient to do so. Effective conservation or control measures must be swiftly executed, and for this to happen the relevant monitoring of the environment (of which the rook is an integral part) must be continuously undertaken. Population counts of the rook are of course easily and cheaply done but problems concerning their population dynamics, especially those outlined in chapter 3 with regard to mechanisms of population growth and dispersion, are not. Other questions which deserve to be answered are those relating to the structure of the population - for example, do rook populations comprise birds all of which are dietary and habitat generalists, or do all the birds differ, each having a particular specialisation? Only when problems such as these have been solved will we be in a

position to advise on acceptable control or management. Having said this, however, the rook has proved notoriously difficult to control (Feare 1974), and it is a measure of its success that despite human persecution for well over 500 years (Murton 1971) it has not only survived but thrived.

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APPENDIX I

The size of N.E. Fife rookeries 1945-1979

The following is a list of rookeries in N.E. Fife. For each rookery its location is given, together with the number of nests it contained in the years 1945, 1975 and 1977 to 1979. The 1945 and 1975 figures are taken from B.T.O. national surveys carried out in those years, and the 1977-1979 data are from the present study. The earliest date of a full survey of N.E. Fife rookeries is 1945 but occasional counts of some rookeries have been made in years other than the above. The results of these are given in footnotes to the table.

I made every attempt to be accurate in counting nests from 1977-1979 (see Chapter 3). The 1945 data are probably very accurate as well, given that they were collected by Rintoul and Baxter, probably the two foremost ornithologists in Scotland at the time, and both of whom lived in Fife. In 1975 the counts were made by several recorders and the exhaustive coverage of the 1945 and 1978 surveys was not attained. So while the counts for each rookery are probably accurate enough the sum of all those counted does not reflect the true breeding population size in that year. The same applies, of course, to the sample counts in 1977 and 1979.

In the table a dash ('-') means that the rookery in question was not included in the survey for the year indicated. With respect to the 1945 survey this probably means that the rookery did not exist. In the other years it means, with a few exceptions, that the rookery did exist but was not censused. Rookery 30/15 which does not appear in the table lies outside the study area.

ROOKERY	REFERENCE NO.	O.S. MAP REFERENCE	NUMBER OF NESTS				
			1945	1975	1977	1978	1979
Montrave Farm	30/01	NO 377067	-	93	-	161	-
Montrave Gardens	30/02	NO 379065	-	16	-	7	-
South of Laundry*	30/03	NO 380063	30	2	-	0	-
Smithygreen Road (A)	30/04	NO 379059	75	11	-	21	-
Smithygreen Road (B)	30/05	NO 378058	-	3	-	29	-
Smithygreen Burn	30/06	NO 372053	-	5	0	0	-
Montrave Lodge	30/07	NO 374052	-	6	-	5	-
Sheelynn	30/08	NO 362043	-	23	-	48	-
Whallyden	30/09	NO 360043	-	11	-	0	-
Balgrummo Farm	30/10	NO 372033	-	8	-	9	-
Pilmuir	30/11	NO 392040	-	100	-	157	-
Cock-my-lane	30/12	NO 369108	691	3	-	2	-
Linnwood Hall	30/13	NO 373017	-	8	-	5	-
Treaton Farm	30/14	NO 326024	-	38	-	122	-
Kettlebridge Chapel	30/16	NO 311071	97	150	-	154	-
Woodburn House	31/01	NO 397112	245	69	-	68	-
Craigrothie	31/02	NO 378105	-	66	-	-	-
Hill of Tarvit	31/03	NO 380120	-	33	-	74	-

*3 nests in 1944 (Rintoul & Baxter)

Tarvit Avenue, Cupar	31/04	NO 383144	-	2	-	0	-
Cults Mill	31/05	NO 342103	-	46	-	0	-
Tarvit Farm	31/06	NO 384142	194	21	-	28	-
Hough Park, Cupar	31/07	NO 377145	32	3	11	9	-
Gilliesfaulds	31/08	NO 358145	-	5	-	-	-
Cunnoquhie Mill Wood	31/09	NO 314165	-	234	316	342	-
Rathillet House	32/01	NO 360208	-	12	4	5	-
Fliskmillan	32/02	NO 302212	-	12	-	16	-
Lochmalony House	32/03	NO 369203	549	82	58	25	-
Luthrie	32/04	NO 332198	-	-	-	52	-
Elie Estate	40/01	NO 491004	10	34	-	31	-
Muircambus	40/02	NO 469023	-	36	-	35	-
Leven Road	40/03	NO 403024	-	15	-	2	-
Beach Hotel	40/04	NO 407025	-	3	-	1	-
Balchrystie House	40/05	NO 459030	131	7	-	7	-
Near Balchrystie	40/06	NO 449031	3	2	-	1	-
Lundin Links Hotel	40/07	NO 411029	95	20	-	20	-
Balhousie	40/08	NO 433062	-	20	-	53	-
South of Falfield	40/09	NO 449082	-	30	-	37	-
Falfield	40/10	NO 445088	757	8	-	12	-
Teasses Lodge (A)	40/11	NO 401081	-	10	-	16	-
Teasses House	40/12	NO 407081	-	186	-	90	-
Northtown of Falfield	40/13	NO 447093	-	3	-	1	-
North of Clockmadron	40/14	NO 425091	-	4	-	-	-

Higham	40/15	NO 466095	-	120	-	91	-
Brewsterwells	40/16	NO 480099	-	40	38	32	24
Boghall Burn	40/17	NO 427073	-	-	-	36	-
Teasses Lodge (B)	40/18	NO 403079	-	-	-	30	-
Seggie	41/01	NO 446190	-	16	-	5	5
Guardbridge	41/02	NO 449192	-	35	-	11	-
Craigfoodie	41/03	NO 407182	559	159	268	272	-
Kincaple	41/05	NO 465184	446	40	-	30	-
Strathtyrum	41/06	NO 491174	143	78	189	-	-
Ladebraes	41/08	NO 498160	-	20	-	-	-
Clatto Hill	41/09	NO 436157	-	40	-	-	-
Kinninmonth	41/10	NO 426123	-	16	-	83	-
Cameron Manse	41/11	NO 484117	-	30	69	51	52
Northbank	41/12	NO 482108	-	15	30	31	29
Lathockar House	41/13	NO 493108	-	20	-	97	63
Cupar Junction	41/14	NO 449190	227	58	-	31	28
Strathtyrum Lodge	41/15	NO 494175	-	0	-	3	9
Golf Course*	41/16	NO 496178	94	-	-	58	-
Kirktonbarns	42/01	NO 451267	-	150	-	105	-
Disused Railway	42/02	NO 450218	-	101	162	139	-
Water Tower	42/03	NO 457214	-	16	0	4	-
Earlshall House**	42/04	NO 466211	528	200	32	61	-
Pusk Farm	42/05	NO 439208	101	14	12	11	-
Pittarthie Castle	50/01	NO 518091	-	12	0	0	0

* 1 nest in 1942, c. 20 nests in 1944 (Rintoul & Baxter)
** > 500 nests in 1950´s (Grierson 1962)

Kingsmuir House	50/02	NO 536085	-	159	-	99	-
Gordonshall Farm	50/03	NO 534068	93	27	-	28	-
Kellie Castle	50/04	NO 520052	312	93	-	112	-
Grangemuir House	50/05	NO 539042	325	195	184	225	-
Balcaskie House	50/06	NO 525037	-	112	-	-	-
West Lodge, Balcaskie	50/07	NO 512033	-	63	72	110	-
Kennedy Gardens	51/01	NO 503165	-	6	-	3	-
Bus Station, St. Andrews	51/02	NO 505167	-	6	10	6	11
St. Leonards, St. Andrews	51/03	NO 512165	145	7	-	5	-
Lade Braes, St. Andrews	51/04	NO 508163	-	7	-	-	-
Kingsbarns Manse	51/05	NO 593120	19	14	15	11	-
Kingsbarns, Sea Road	51/06	NO 595118	-	25	26	41	-
Grange	51/07	NO 518139	-	-	-	64	-
Kilduncan	51/08	NO 574117	-	-	-	84	-
Kippo Farm (A)	51/09	NO 581103	-	-	-	178	-
Kippo Farm (B)	51/10	NO 579105	-	-	-	27	-
Kippo Pines	51/11	NO 572101	-	-	-	136	-
Dunino	51/12	NO 541108	241	-	-	102	119
Brownhills	51/13	NO 527151	-	-	-	-	-
Wormistone House	60/01	NO 612095	764	101	116	154	-
Wormistone Farm	60/02	NO 614093	-	3	0	0	-
Crail Church	60/03	NO 614080	123	14	12	9	-

*13 nests in 1976

APPENDIX II

The geology and altitude of N.E. Fife rookeries and the species of trees in which nests were contained in 1978

The following list of N.E. Fife rookeries known to exist in 1978 includes the altitude (to the nearest 25 feet) of each, the geological substratum on which it stands and the genera of trees in which the nests counted in that year were contained. English names of trees are: Fagus- beech; Acer- sycamore; Ulmus- elm; Quercus- oak; Fraxinus- ash; Aesculus- horse chestnut; Pinus- pine; Picea- spruce; Larix- larch; Araucaria- Chile pine; Cupressus- cypress. More than one species within most of these genera may be represented in the table.

ROOKERY	REFERENCE NO.	GEOLOGY	ALTITUDE	TREE SPECIES
Montrave Farm	30/01	Dolerite	600	Fagus-103 Acer-4 Ulmus-8 Quercus-46
Montrave Gardens	30/02	Dolerite	550	Fagus-1 Acer-6
South of Laundry	30/03	Dolerite	575	No nests
Smithygreen Road (A)	30/04	Dolerite	425	Fagus-16 Quercus-2 Pinus-3
Smithygreen Road (B)	30/05	Dolerite	400	Pinus-29
Smithygreen Burn	30/06	Dolerite	425	No nests
Montrave Lodge	30/07	Dolerite	425	Fagus-5
Sheelynn	30/08	Carboniferous Limestone	350	Fagus-29 Acer-13 Quercus-5 Pinus-1
Whallyden	30/09	Carboniferous Limestone	450	No nests
Balgrummo Farm	30/10	Carboniferous Limestone	300	Acer-9
Pilmuir	30/11	Carboniferous Limestone	300	Fagus-9 Pinus-148
Cock-my-lane	30/12	Coal Measures	125	Acer-1 Ulmus-1
Linnwood Hall	30/13	Coal Measures	100	Fagus-3 Acer-1 Fraxinus-1
Treaton Farm	30/14	Millstone Grit	350	Fagus-1 Acer-6 Ulmus-3 Quercus-24 Pinus-88

Kettlebridge Chapel	30/16	Calciferous Sandstone	250	Fagus-54 Acer-26 Ulmus-52 Fraxinus-13 Aesculus-2 Unidentified-7
Woodburn House	31/01	Calciferous Sandstone	300	Fagus-44 Quercus-6 Pinus-18
Craigrothie	31/02	Dolerite	400	Not counted
Hill of Tarvit	31/03	Dolerite	425	Acer-35 Pinus-39
Tarvit Avenue, Cupar	31/04	Old Red Sandstone	75	No nests
Cults Mill	31/05	Old Red Sandstone	125	No nests
Tarvit Farm	31/06	Old Red Sandstone	100	Quercus-4 Pinus-24
Hough Park, Cupar	31/07	Old Red Sandstone	75	Acer-5 Ulmus-3 Aesculus-1
Cunnoquhie Mill Wood	31/09	Andesitic Lavas	500	Fagus-44 Fraxinus-1 Pinus-225 Picea-31 Larix-41
Rathillet House	32/01	Andesitic Lavas	225	Pinus-5
Fliskmillan	32/02	Andesitic Lavas	375	Pinus-16
Lochmalony House	32/03	Andesitic Lavas	300	Fagus-7 Acer-16 Ulmus-2
Luthrie	32/04	Andesitic Lavas	300	Pinus-52
Elie Estate	40/01	Calciferous Sandstone	50	Fagus-12 Acer-3 Ulmus-11 Pinus-5
Muircambus	40/02	Carboniferous Limestone	75	Fagus-8 Acer-13 Ulmus-11 Quercus-3
Leven Road	40/03	Coal Measures	25	Acer-1 Ulmus-1

Beach Hotel	40/04	Coal Measures	50	Fagus-1
Balchrystie House	40/05	Carboniferous Limestone	125	Fagus-5 Acer-2
Near Balchrystie	40/06	Carboniferous Limestone	150	Ulmus-1
Lundin Links Hotel	40/07	Coal Measures	50	Fagus-20
Balhousie	40/08	Dolerite	525	Pinus-53
South of Falfield	40/09	Carboniferous Limestone	675	Fagus-37
Falfield	40/10	Carboniferous Limestone	625	Fagus-12
Teasses Lodge (A)	40/11	Dolerite	575	Acer-16
Teasses House	40/12	Dolerite	625	Fagus-44 Acer-32 Ulmus-1 Quercus-13
Northtown of Falfield	40/13	Carboniferous Limestone	600	Fagus-1
North of Clockmadron	40/14	Carboniferous Limestone	500	No nests
Higham	40/15	Dolerite	525	Fagus-79 Pinus-12
Brewsterwells	40/16	Calciferous Sandstone	600	Fagus-32
Boghall Burn	40/17	Dolerite	500	Fagus-31 Quercus-1 Pinus-4
Teasses Lodge (B)	40/18	Dolerite	550	Pinus-30
Seggie	41/01	Old Red Sandstone	75	Fagus-5
Guardbridge	41/02	Old Red Sandstone	75	Fagus-11

Craigfoodie	41/03	Andesitic Lavas	350	Fagus-43 Acer-102 Ulmus-46 Quercus-13 Fraxinus-13 Pinus-55
Kincaple	41/05	Calciferous Sandstone	75	Fagus-5 Acer-17 Ulmus-8
Strathtyrum	41/06	Calciferous Sandstone	50	Not counted
Ladebraes	41/08	Calciferous Sandstone	50	Not counted
Clatto Hill	41/09	Calciferous Sandstone	500	Not counted
Kinninmonth	41/10	Carboniferous Limestone	250	Quercus-23 Pinus-60
Cameron Manse	41/11	Calciferous Sandstone	550	Fagus-15 Acer-2 Ulmus-6 Pinus-28
Northbank	41/12	Calciferous Sandstone	500	Acer-8 Pinus-23
Lathockar House	41/13	Calciferous Sandstone	500	Pinus-97
Cupar Junction	41/14	Old Red Sandstone	50	Fagus-31
Strathtyrum Lodge	41/15	Marine Alluvium	0	Fagus-3
Golf Course	41/16	Marine Alluvium	0	Acer-2 Pinus-56
Kirktonbarns	42/01	Andesitic Lavas	125	Pinus-105
Disused Railway	42/02	Old Red Sandstone	50	Pinus-139
Water Tower	42/03	Marine Alluvium	50	Fagus-4
Earlshall House	42/04	Marine Alluvium	25	Fagus-33 Acer-15 Ulmus-8 Quercus-4 Pinus-1

Pusk Farm	42/05	Old Red Sandstone	75	Fagus-4 Acer-7
Pittarthie Castle	50/01	Calciferous Sandstone	475	No nests
Kingsmuir House	50/02	Calciferous Sandstone	400	Pinus-99
Gordonshall Farm	50/03	Calciferous Sandstone	300	Fagus-11 Quercus-17
Kellie Castle	50/04	Calciferous Sandstone	200	Fagus-22 Acer-44 Ulmus-6 Quercus-40
Grangemuir House	50/05	Calciferous Sandstone	100	Fagus-49 Aesculus-9 Pinus-154 Araucaria-9 Cupressus-4
West Lodge, Balcaskie	50/07	Calciferous Sandstone	75	Fagus-48 Acer-40 Ulmus-14 Quercus-8
Kennedy Gardens	51/01	Calciferous Sandstone	25	Fagus-3
Bus Station, St. Andrews	51/02	Calciferous Sandstone	25	Fagus-2 Acer-4
St. Leonards, St. Andrews	51/03	Calciferous Sandstone	25	Fagus-1 Acer-2 Aesculus-2
Lade Braes, St. Andrews	51/04	Calciferous Sandstone	50	Not counted
Kingsbarns Manse	51/05	Calciferous Sandstone	100	Fagus-8 Acer-2 Pinus-1
Kingsbarns, Sea Road	51/06	Calciferous Sandstone	75	Fagus-18 Acer-8 Ulmus-2 Pinus-13
Grange	51/07	Calciferous Sandstone	275	Pinus-64
Kilduncan	51/08	Calciferous Sandstone	125	Fagus-28 Acer-52 Ulmus-1 Fraxinus-3

Kippo Farm (A)	51/09	Calciferous Sandstone	225	Acer-10 Fraxinus-3 Pinus-165
Kippo Farm (B)	51/10	Calciferous Sandstone	225	Fagus-12 Acer-15
Kippo Pines	51/11	Calciferous Sandstone	250	Pinus-136
Dunino	51/12	Calciferous Sandstone	300	Fagus-62 Acer-14 Ulmus-7 Fraxinus-2 Pinus-17
Brownhills	51/13	Calciferous Sandstone	200	Not counted
Wormistone House	60/01	Calciferous Sandstone	150	Fagus-116 Acer-11 Ulmus-10 Fraxinus-3 Picea-14
Wormistone Farm	60/02	Calciferous Sandstone	150	No nests
Crail Church	60/03	Calciferous Sandstone	100	Acer-9